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ON THE MARINE FAUNA OF GHANA

BY

R. BASSINDALE

Department of Zoology, University of Bristol

[Accepted 14th February 1961]

(With 5 figures in the text)

A general survey of the marine fauna of the Gold Coast (now Ghana) was carried out in the years 1949–52. Collections were made along the whole length of the Ghanaian coast line and in the sub-littoral near Accra. Systematic descriptions have already been published of the Polychaeta ; Pagurida ; Hippidea and Brachyura ; Echinodermata and Tunicata. Accounts of the Cirripedia ; Caridea, Palinura and Thalassinidea ; and Polyzoa are expected shortly, while accounts of the Porifera and some Coelenterata will be delayed. Lists of the Mollusca (excluding Cephalopoda) and fishes are given here in Appendices 4 and 5.

In all, 586 species have been named, including 25 new species and many new records for the area. There are differences in the intertidal fauna at the east end of the coast as compared with the west, and there are similar changes in the sub-littoral fauna in the few miles from Accra to the Densu mouth.

The distribution of sub-littoral animals conforms with Buchanan's (1958) description of the zonation, but no evidence was found of his mollusc-free zone (Buchanan 1954).

The fauna consists mainly of the West African tropical species with a strong representation of species found further north and a few which extend southwards. There is also a small element of tropical species found also on the American Atlantic coast and a few pan-tropical species.

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Fig. 1—A map of the Ghana coastline showing the collecting stations listed in Appendices 1 and 3.

the variety of animals present and to establish a type collection at the College for the use of future workers in this field. The collections were sorted and despatched to various systematists who have published lists of species and have sent to the College named specimens from the collections.

Work on the shore was limited to the general collecting by hand of macroscopic species and most of the collections were made in rocky places which varied from steep rock faces to extensive boulder and gravel strewn flats. Stations were selected along the whole length of the Ghanaian coastline (Appendix 1 and Fig. 1) and each was explored during at least two periods of spring tides.

The investigation of the sublittoral fauna was made from a 31-foot motor boat, purchased for the work by the College and delivered in time for only a limited survey of the bottom near Accra. The dredges and Agassiz trawl used were designed and made at the College. The 90 stations worked are shown in Fig. 2 and listed in Appendix 2.

Additional specimens were obtained from other places by various means and these sources are described in Appendix 3.

RESULTS

Naturally many thousands of specimens were taken and of the groups so far studied 586 species have been named, including 25 new species and many new records for Ghana and for West Africa.

Porifera and Coelenterata

Sponges were not common on the soft bottoms of the Accra sub-littoral, but numerous growths were present on partly sheltered rocky shores.

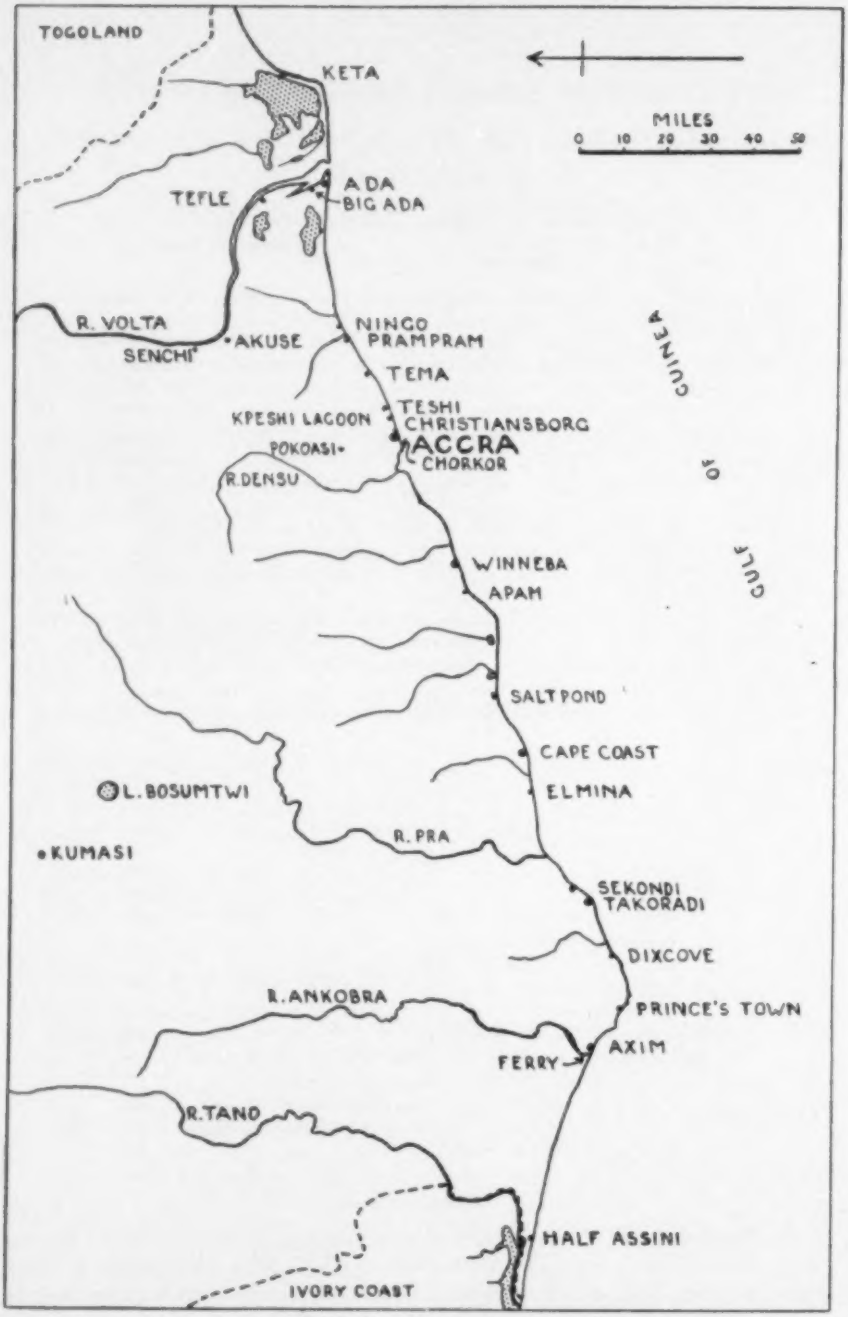
Among coelenterates the most notable feature was the extensive intertidal growths of colonial zoanthid anemones which covered extensive areas of rocky and stony shores and which were zoned below the barnacles. Extremely good developments were noticed at Dixcove and Axim.

Although the area is a tropical one, it is situated on the " cold " side of the Atlantic and coral reefs do not occur. A few small specimens of madreporarians and a rather greater abundance of sea fans (Alcyonarians) subscribe little more to the Ghanaian fauna than they do to the British fauna. The Madreporaria and hydroids have been commented on by Buchanan (1953 and 1957 b).

Floating species were not specially investigated, but it is known that small medusae and siphonophores are quite common in the plankton, and *Physalia*, although not abundant, does occur. *Velella* was not seen. Scyphozoan jellyfish are rather spasmodic in their occurrence and no dense shoals were ever seen although on one occasion in a few metres of water a dredge full of jellyfish suggested the presence of a bottom-living species off Labadi (near Accra). Unfortunately the systematic examinations of the sponges and coelenterates collected during the survey have not been completed so that no detailed reports are yet available.

Annelida

No oligochaetes or leeches were taken in the present survey, but polychaetes were a notable feature of the fauna and the 37 tidal and 34 sub-littoral species collected have been described by Tebble (1955).



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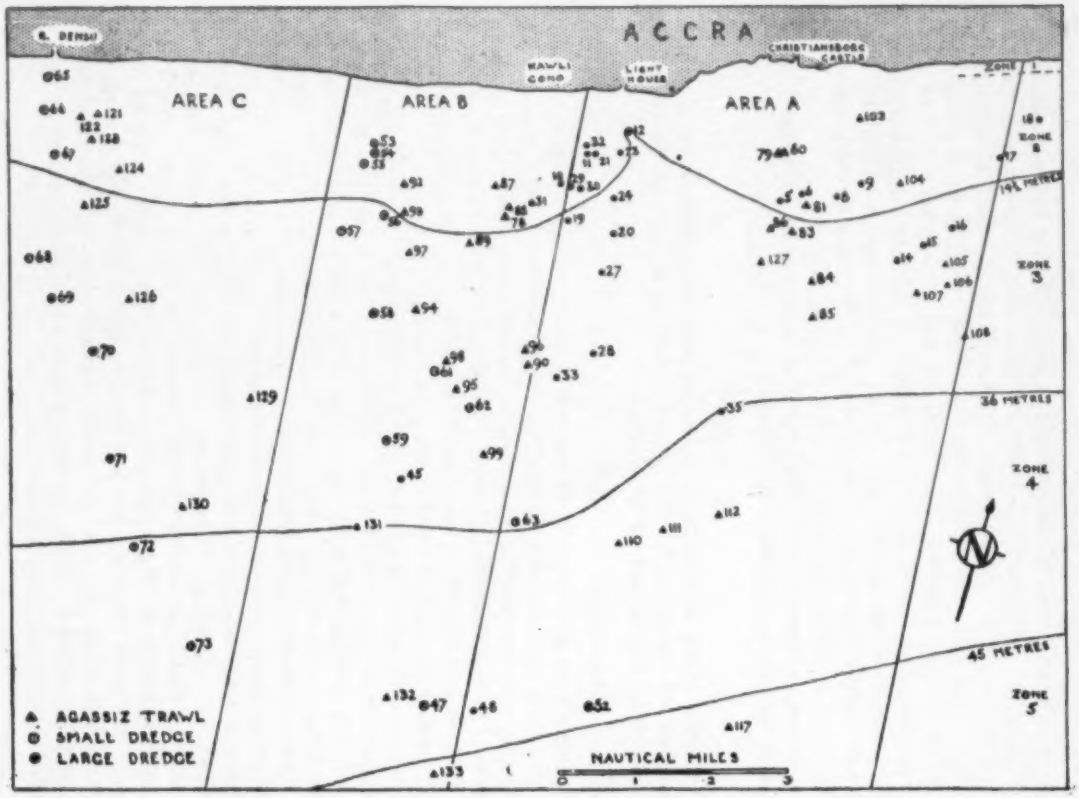

Fig. 2—A chart of the Ghana coastline near Accra showing the sub-littoral collecting stations listed in Appendix 2, and the division into Zones 1 to 5 and areas A, B, and C (see text).

Cirripedia

The present collection of 15 species of barnacles has been examined and will be reported on by Dr H. G. Stubbings. Gauld (1957) listed 13 species for the Ghana coast and of these four were not taken in the present survey, but new records of species or varieties were made as follows :—

Lepas hilli Leach
Smilium renei Gruvel
Chthamalus sp. (not yet determined)
Chthamalus stellatus stellatus (Poli)
Balanus amphitrite pallidus Darwin
Balanus amphitrite (variety not yet determined)
Balanus fallax Broch
Tetraclita divisa Nilsson-Cantell
Kochlorine sp. (not yet determined)

The total number of species recognized thus becomes 19 and of these *Chthamalus stellatus* is represented by two varieties, and *Balanus amphitrite* by four. The common shore barnacle is *Chthamalus dentatus*.

Prawns (Caridea, Palinura, Thalassinidea)

The detailed account of the prawns is nearly ready for publication and Dr L. B. Holthuis has identified 37 species from the collection, of which 21 are intertidal and 16 sub-littoral. A notable feature of the intertidal fauna is the large number of individuals and species of the snapping prawns (*Alpheus* spp. and others), while some of the ordinary prawns are sufficiently abundant in the sub-littoral to be fished and marketed (e.g. *Palaemon hastatus*).

Hermit Crabs (Pagurida)

Hermit crabs are a notable feature of the fauna and some species are very common. The collection included 6 intertidal and 12 sub-littoral species which have been described by Dr J. Forest (1956) with a separate note on the post-larval stages of one species (Forest, 1954).

Crabs (Hippidea and Brachyura)

Crabs are abundant and varied in the Ghanaian fauna and Professor Th. Monod has included his determination of the crabs from the present collection in a monograph of the West African species as a whole (Monod, 1956). He lists 27 intertidal and 27 sub-littoral species from the present survey.

Molluscs (excluding the Cephalopoda)

The present survey included 167 species of shelled molluscs, of which 77 are intertidal and 90 sub-littoral. The group is of extreme importance in the marine environment and it tends to dominate the Ghanaian fauna. The species *Turritella annulata* is found in vast numbers in Zone 3 (see below) and the abundance of limpets and winkles is no less marked on Ghanaian shores than elsewhere in the world. Buchanan (1954) has given a check list of 159 (living) species from the same area as covered by the present survey and in a

subsequent list (Buchanan & Anderson, 1955) has added 94 more species. The records for the present survey are given in Appendix 4.

Polyzoa (=Bryozoa)

Not all the polyzoa have yet been determined but Dr A. B. Hastings has provided information on 15 intertidal and 19 sub-littoral species from the present survey and will be publishing a detailed account later. The group is well represented and extensive growths occur in the fifth (or Bryozoan) Zone below 45 metres where they and other calcareous growths provide a habitat for a very varied deep water fauna.

Echinodermata

Dr A. M. Clark has published a list of the 36 species of echinoderms collected during the survey (Clark, 1955), of which 12 are intertidal and 24 sub-littoral. Of these the sand star *Astropecten michaelsoni* is abundant in moderate depths in the sub-littoral (7-51 metres), while the echinoid *Echinometra lucunter* is extremely abundant in the lithothamnion zone of fairly exposed rock shores at the western end of the coastline, notably at Prince's Town.

Tunicata

Of the fifteen species of ascidian collected during the survey, 12 are intertidal and 3 sub-littoral. Millar (1953) has included in his account other specimens collected from Ghana and of the 26 species listed 12 were already known, 13 are new species, and one is a new subspecies.

Fishes

An extensive collection of fishes was not attempted, but over 1,000 specimens were taken and have been determined by Dr J. Cadenat. A list is given in Appendix 5 and this includes three new species and 54 new records for Ghana. However, as the collection was not comprehensive the fishes are not included in the general survey of the fauna given below.

DISCUSSION

Although the marine fauna of West Africa, and particularly of Ghana, has been little known in the past, the long series of investigations by the Institut francais d'Afrique Noire at Dakar, the Atlantide Reports (1950–59) the paper by Longhurst (1958), and the recent series of papers from Ghana referred to in the present account, are rapidly changing the situation.

The general distribution of species

The balance of the fauna can be compared, for those groups studied, with the numbers of species of the same groups at Plymouth (Plymouth Marine Fauna, 1957). It will be seen (Table 1) that hydroids, barnacles, molluscs, and perhaps polyzoa, contribute similar proportions of species to the two faunas but polychaetes and tunicates are less important. This discrepancy is quite possibly due to the less intensive collecting in Ghana but the greater importance of the Crustacea (prawns, hermit crabs, and crabs) and the echinoderms is almost certainly due to the greater variety of these groups on this tropical coast.

With regard to the bathymetric distribution of the fauna, the main feature is the isolation of the intertidal and sub-littoral fauna. Very few species indeed have been found in both situations, and although the occupation of both habitats is usually restricted to a small proportion of the marine fauna the extreme isolation shown here is probably due to the fact that shore collecting was mainly on rocky shores, while the sub-littoral collections were made on soft bottoms.

Table 1—A comparison of the number of species in Ghana and at Plymouth for selected groups

Group	Number of species				Percentages	
	Ghana			Plymouth	Ghana	Plymouth
	Littoral	Sub-littoral	Total	Total		
Hydroids (from Buchanan 1957b)	13	37	50	99	10	9½
Polychaetes	37	34	71	262	14½	25
Barnacles	8	6	14	21	2½	2
Prawns	21	16	37	32	7½	3
Hermit crabs	6	12	18	7	3½	½
Crabs	27	27	54	56	11	5½
Molluscs	77	90	167	345	34	33
Polyzoa	15	19	34	121	7	11½
Echinoderms	12	24	36	47	7½	4½
Ascidians	12	3	15	65	3	6
TOTAL	228	268	496	1,055	100½	100½

For intertidal plants, Lawson (1956) has suggested that, although the general ecological conditions might be assumed to be similar along the whole of the Ghanaian coastline, some species are differentially distributed. Accordingly, the present data on the animals have been divided into three classes—those found only in the eastern half (Prampram to Apam) ; those found only in the western half (Dixcove to Axim) ; and those found in both halves. These groups are compared with Lawson's figures for the plants (Table 2).

Thus, for Lawson's plants, 51 per cent occurred only in the eastern half, 13 per cent in the western half, while 36 per cent occurred in both halves. The figures for the grouped totals of the invertebrate animals of the present survey and for Buchanan's survey of the molluscs (and my own figures for the molluscs are similar) indicate that Lawson's suggestion also applies to the animal species. It could be argued that the higher numbers of species found in the eastern half (where all three observers lived) was due to the more intensive collecting on easily reached shores. But this merely serves to emphasize the absence from the eastern end of the 46 species found in the west and not in the east. It seems clear that there is some gradient in ecological

conditions along the coast which may in fact be due to the greater abundance of rocky shores in the western half.

Table 2—The east to west distribution of the Ghanaian intertidal fauna and flora

Area inhabited	Numbers of species			Percentage of total		
	All invertebrates of present survey	Molluscs Buchanan's survey (1954)	Plants Lawson's survey (1956)	All invertebrates of present survey	Molluscs Buchanan's survey (1954)	Plants Lawson's survey (1956)
Eastern half	80	24	50	39	41	51
Western half	33	8	13	16	14	13
Both halves	91	27	36	45	46	36
Total	204	59	99	100	101	100

Zonation of intertidal species

A general account of the zonation of the intertidal animals and plants of Ghana is available in the works of Buchanan (1954), Lawson (1956), and Gauld & Buchanan (1956, 1959). In addition Lawson (1957) has made a valuable contribution to our knowledge of the factors influencing intertidal zonation in his account of the seasonal variation of levels produced by the peculiar tidal regime of the Ghana coast.

One of the main features of the zonation described is the upward displacement of zones due to the constant wave wash to which the Ghanaian coast is subjected. In the above accounts, although frequent reference is made to this phenomenon, no particularly good example including tide levels is illustrated nor are measurements of abundance given. Accordingly, a survey of a moderately exposed rock coast at Winneba is given here.

Zonation at Winneba

The section was made on a uniform rock slope with the aid of two metre-rods and a spirit level. Counts were made at intervals with a wooden square of 50 cm. side or, for barnacles, with a wire frame of 10 cm. side. An approximate estimate of the level of low water had to be made as the wave wash made accurate determination difficult. The section contour is given in Fig. 3 and, except for the flattening out near low water, the rock slope was very uniform at 30°. The abundance and distribution of the rather poor fauna is also illustrated. It will be seen that five of the species present occur only above H.W.M., while the four most abundant species all extend above H.W.M. and two have their greatest abundance above this level. The supra-littoral fringe thus extends to at least 2·85 metres above H.W.M. (Lawson (1956) quotes examples from more exposed shores where this extension is much greater) and the " mid-littoral " itself extends well above high water level.

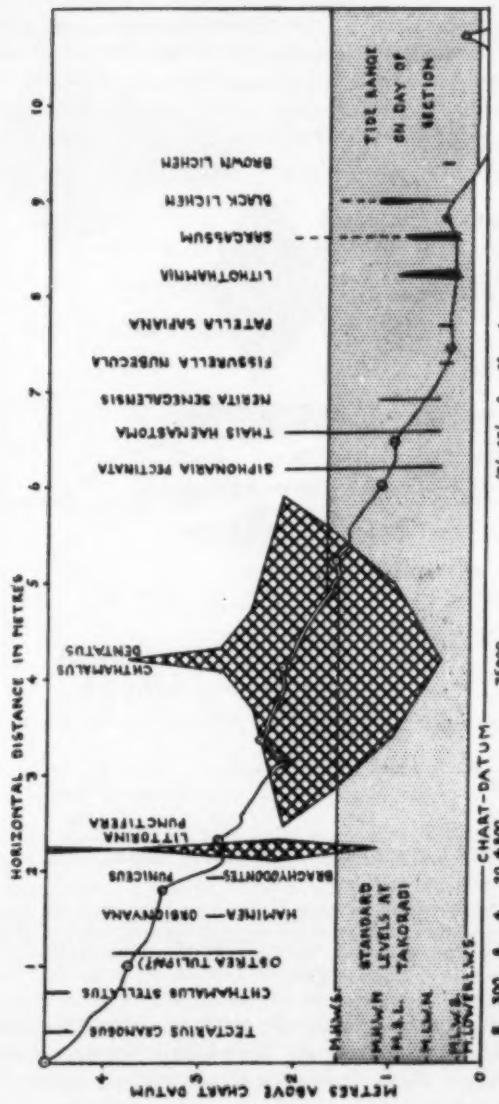

Fig. 3—A diagram of a rock section at Winneba showing the distribution and abundance of intertidal species. Sampling stations are indicated by small circles : vertical distribution by the vertical extent of the diagrams for each species and abundance by the width of these same diagrams. The range of tide is shown by the stippled areas.

Zonation at Tenpobo (near Prampram)

Although quite unlike the coast at Winneba, the intertidal region at Tenpobo has features of interest. The extensive beach consists mainly of a triangular reef extending seawards for a distance of 230 metres. The first 30 metres consists of a steep sand slope but after this a fairly level stony plain extends for 200 metres. Gauld & Buchanan (1959) have described the animal zonation in general terms but a section taken in February 1950 illustrates the zonation in a more specific way. The slope of the beach was determined by observations of water level at stations 20 metres apart (Fig. 4) and it was found

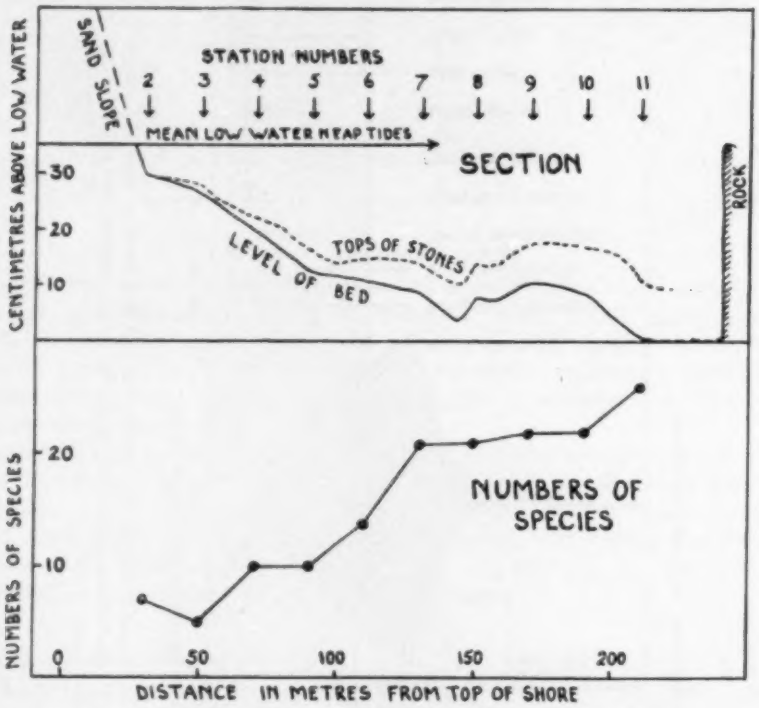

Fig. 4—Diagrams showing the contour and variety of species on a section of the stony beach at Tenpobo, near Prampram. The upper diagram shows the collection stations and the slope of the beach with an indication of the sizes of stones. The lower diagram shows the increasing number of species present as low water level is approached.

that the level at the landward edge was about 30 cm. above low water level and dropped regularly until at 170 metres it was about 10 cm. Between 170 and 190 metres there was a slight depression a few centimetres deep. Subsequently, the level rose slightly to a level between 180 and 200 metres of 10 cm. after which it fell away to L.W. level at 230 metres. The whole shore is protected from low tide wave wash by rocks rising to 30 or 40 cm. above L.W. level and distributed irregularly along the seaward edge of the reef.

The numbers of species at the various stations and the abundance and distribution of the commoner species are illustrated in Figs. 4 and 5.

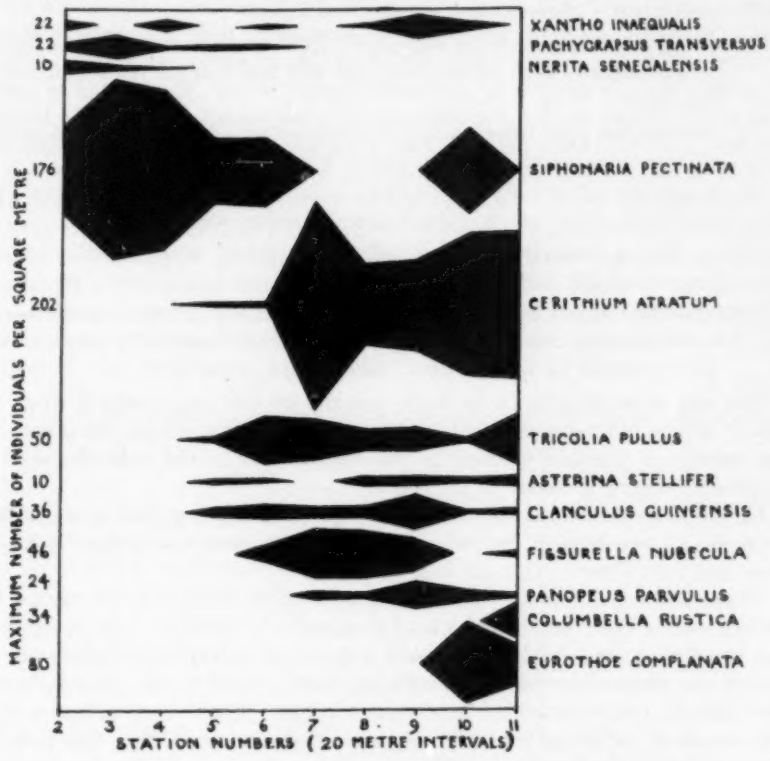

Fig. 5—Diagrams (all to the same scale) showing the distribution and abundance of the commonest species across the Tenpobo beach below low water of neap tides.

For most of the stony area there is a local difference in level between the tops and bottoms of the stones (which rest on smaller materials—gravel, sand or mud) of the order of 10 to 25 cm. Despite this local variation and the gentle and irregular nature of the slope down to L.W.M. the animals are clearly distributed by zones. Some of them (*Xantho inaequalis*) extend across the whole flat but most of them are either abundant near the landward fringe and die out to seawards or are abundant near L.W.M. and die out on the upper parts of the flat to landwards. It is surprising that the zonation should be so clearly marked where local irregularities in level are so much greater than the general slopes to seawards.

Zonation of sub-littoral species

Detailed accounts of the depths at which the sub-littoral animals of the present survey have been found is given in the works already cited.

Buchanan (1958) has described the distribution of the sub-littoral fauna of the Accra area in terms of five communities occurring in gradually increasing depth zones parallel to the shore and dependent on the differing composition of the substratum. These zones he names as follows :—

1. *Transition community or surf zone :* from low-water mark to a depth of 3·5 metres. Surf action is severe and the bottom is of medium to fine sand.
2. *Inshore fine sand community or* Cultellus *zone :* from 5·5 to 14·5 metres with some wave disturbance and a bottom of fine sand.
3. *Sandy silt community or* Turritella *zone :* from 14·5 to 36 metres with negligible wave action and a bottom of sandy-silt.
4. *Silty-sand community :* from 36 to 45 metres with a rather mixed bottom of silt and coarse sand.
5. *Offshore coarse sand community or bryozoan zone :* from 45 to 90 metres with a calcareous rock and sand bottom covered to a large extent with growths of foraminifera, corals, and polyzoa.

The surf zone is difficult to work and no records are available from the present survey but using the depth limits given by Buchanan for the remaining four zones it is possible to describe the distribution of the animals taken in the present survey in terms of his zones.

Of the 225 sub-littoral species so far determined, 45 per cent occur in only one zone, 33 per cent in two adjacent zones, 19 per cent in three adjacent zones and only 3 per cent in all four zones.

Thus, bearing in mind that the Agassiz trawl and to some extent the dredges used in the present survey tend to sample the epifauna more extensively than the infauna on which Buchanan's account is mainly based, and that the area of the present survey was somewhat more extensive, the present figures offer striking confirmation of Buchanan's zones. There is of course a large proportion of the fauna that occupies more than one zone, but this is to be expected, particularly of the epifauna and is noticeable in the hermit crabs (see Fig. 2, Forest, 1956).

Nevertheless, there are three features of interest. Although *Turritella annulata* is dominant and is almost diagnostic of Zone 3, it does occur in all four zones and sometimes in reasonable numbers. It has been found from 10 to 64 metres. Other species are also widespread.

The area that was intensively investigated by Buchanan is illustrated in Fig. 2 (Area A). According to Buchanan, stations west of this area had a similar fauna and zonation. However, as the area west of the Densu is known to include stony bottoms, the results of the present survey were analysed to determine whether in fact there was any change in the trawl and dredge fauna from east to west. After eliminating zones 1 and 5, for which too few records are available for comparative purposes, the fauna of zones 2, 3 and 4 have been grouped into Area A (Buchanan's area off Accra), Area B off Korle Gonno, and Area C, still further west off the mouth of the Densu (Fig. 2). The total number of species thus recorded are Area A 127, Area B 158, Area C 116. Table 3 illustrates the distribution of these species.

It seems clear from the high proportion of species which are restricted to one or to two adjacent zones (54 per cent) that there is a change in the population from east to west over a relatively small distance and Buchanan has already noted a more drastic change in the zonation found off Takoradi. A third feature of the collection is that numerous molluscs were found between 36 and 45 metres. Buchanan (1954, p. 32) says that this zone is apparently devoid of living molluscs. Of the 90 species recorded in the sub-littoral during the present survey, four species occurred in zones 2–5, 16 occurred in three zones (including zone 4), and 16 occurred in two adjacent zones (either 3 and 4, or 4 and 5), while nine species were recorded only from zone 4. Thus, 45 living species occurred in depths ascribed by Buchanan to zone 4, compared with 24 in zone 2, 53 in zone 3, and 39 in zone 5. This discrepancy in results may well be due to variation in the depths to which the *Turritella* zone (No. 3) extends and to the extension of the bryozoan zone (No. 5) into shallower depths than 45 metres, but as the general analysis of the present results fits the zonation described by Buchanan (see above) it seems that the mollusc-free zone can only be a very local phenomenon.

Table 3—The distribution of species in the three areas A, B, and C, from east to west

Areas	Number of species	Percentage numbers
In all three areas	68	33
In A and B, not in C	32	15
In A and C, not in B	6	3
In B and C, not in A	17	8
In A only	21	10
In B only	39	19
In C only	25	12
Total	208	100

Longhurst (1958) has given a very valuable account of both the intertidal and the sub-tidal fauna of Sierra Leone and adjacent territories. His shore sections amplify our knowledge of the intertidal (and estuarine) distribution of animals on the West African coasts and his sub-tidal survey was much more extensive than the present and Buchanan's surveys. Longhurst's division of the fauna of soft bottoms into communities does not entirely agree with Buchanan's and it is probable that more work is required before the two classifications can be integrated.

Geographical distribution

Detailed analyses of the geographical distribution of the various groups are to be found in the literature already cited, but it may be said that in general the Ghanaian fauna consists largely of West African tropical species with a strong representation of more northerly species. There is a much smaller group of species which have been found in South-West or South Africa, and a

somewhat similar group of species from the eastern Atlantic. Only a small percentage occur in other oceans and these are mainly pan-tropical species.

Thus the records of the present survey include 61 per cent of species already known from tropical West Africa together with 16 per cent of species already known from the more northerly West African coast and 11 per cent from more southerly coasts. This represents a total of 88 per cent of West African species in the Ghanaian fauna, the remaining 12 per cent including new, eastern Atlantic, and pan-tropical species.

Acknowledgments

Apart from the firm support given by the University College itself to the development of the marine investigations (and this includes Mr Damptey of the engineering workshop who made the dredges and trawls and other equipment, and the Clerk of Works (Mr Eichenberg and later Mr Smallridge) who maintained the transport and built the net store in Accra), I wish to thank sincerely the numerous outside authorities who smoothed the path of development. Notable among these was the Chief Fisheries Officer, Mr F. R. Johnson (now in Nigeria), who, in addition to giving frequent and sound advice, permitted his staff (notably Mr Livingstone and Mr B. Quaye) to receive the launch, to lay moorings, to service the boat, to engage and supervise the African crew, and to provide various materials difficult to obtain. Among others, mention must be made of the Customs and Railway Officials for various concessions connected with our use of the Accra Harbour facilities, including permission to erect a net store in the harbour precincts; of the Agricultural Department, the Survey Department, the Public Works Department, and the Marine Surveyor's Department at Takoradi, who all contributed advice and material aid appropriate to their special fields; of the various District Commissioners in whose territories I worked, for permission to use their Rest Houses; and of the Prisons Department for the collection of specimens by their staff from their seine net at Chorkor. The most pleasant feature of my work in Ghana was the willing and welcoming attitude of all the people with whom I came in contact, whether government officials or African chiefs and their peoples. The Ghanaian meets life with a broad smile and it was a great pleasure to have worked with him. Special among these I should like to thank my friends, the loyal assistant Mr Ebenezer T. Totimeh, the departmental driver Mr Ofori, my crew supervisor Mr B. Quaye, and Mr Mensah of Oblogo, for the many happy hours I spent in their company.

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APPENDIX 1

List of the main, intertidal collecting stations. (Geological notes by Professor W. J. McCallien.) See Fig. 1.

Ningo. See Prampram.

Tenpobo. See Prampram.

Prampram, 24 miles east of Accra. The coast is of sand and the upper three-quarters of the beach is a steep sand slope. Near the headlands of a series of shallow bays there are low level rock and boulder reefs extending out to sea. These occupy the lowest foot of the spring tide range (and are not exposed on all tides) except for native rock which may rise several feet above this level.

At *Ningo*, just over two miles east of Prampram, the reef is mainly of native rock with a few boulders.

At *Tenpobo*, one and a half miles east of Prampram, the reefs are protected from low level wave wash by a line of slightly higher rocks to seaward.

The reef has many small boulders and stones, usually packed in sand or gravel.

No collecting was done at Prampram itself although there are reefs just west of the town. Collections in the present survey were made on the Tenpobo reefs although the name Prampram is retained as it is easier to find on the map. The rocks at Ningo and Tenpobo are members of a mixed assemblage of siliceous and micaceous gneisses typical of the Ghanaian Archean. The different types are intimately interbanded and the whole assemblage has the appearance of being a sedimentary group.

Christiansborg, 2 miles east of the Accra lighthouse, now really part of Accra. The reefs lie at the foot of the Castle and consist of native rock with small deep pools and deep clefts. Most of the reef is covered at mid-tide level but there are high level rocks with a few species, separated from the low richly inhabited reef by intervening sand. The pools and clefts have dense growths of sessile species. The rocks are well bedded sandstones of Upper Palaeozoic age.

Winneba, 32 miles west of Accra. The beach here is a rock face extending from below low tide level to above high tide level and consists of Winneba granite with many related veins and minor intrusions of granitic material.

Apam, 39 miles west of Accra. The beach is of rocks and boulders set in sand, with rock pools. Eastwards there is a shallow sand bay with sandy mud in the shelter of the headland and the river Brusheng enters the sea through a narrow break in the sand barrier behind which lies a fairly extensive estuary. The rocks are a series of green rocks of hornblendic schists and epidiorite intrusions belonging to the Birrimian System.

Sekondi, 113 miles west of Accra. Here collections were made on the horizontal surface of a rock plateau at or above high tide level. The waves wash over the plateau at most states of the tide and so replenish the pools. The rock is well bedded sandstone of the Sekondi System of the Palaeozoic.

Dixcove, 131 miles west of Accra. An almost square bay with steep sides of approximately 400 yards length is here indented into the coastline. On the east side no collections were made on the large, wave-washed boulders. The west side is more sheltered with small boulders and stones and the inner side has a sand beach with large boulders and native rock mainly below mid-tide level. The rocks of Dixcove granite are a porphyritic grandiodorite with conspicuous phenocrysts of white plagioclase and occasional hornblendes.

Prince's Town, 142 miles west of Accra. A solid rocky headland very much exposed with a few boulders to the east. The rocks are beautifully jointed and break or weather in great slabs of granodiorite similar to the Dixcove granite but more granitic in texture and with mica as well as hornblende.

Axim, 154 miles west of Accra. A low level reef of gravel, sand and mud juts out seaward to rise into a small island and then, further out where it consists of larger stones and boulders it forms Bobowasi Island on which the lighthouse stands. To the east lies a flat bottomed bay about breast deep at low tide and about a quarter of a mile westward a narrow neck of land juts out seaward and extends as an intertidal reef of rock, boulders and stones. The rocks are green rocks, epidiorites and amphibolites, and collecting was done on the

exposed side of the western reef (called by me, the hospital reef H.R.), and mainly on the sheltered side of the lighthouse reef (L.H.R.).

APPENDIX 2

List of sub-littoral collecting stations. (See Fig. 2). (Numbers missing represent plankton or other stations not relevant to the bottom fauna stations.) Dredge hauls were of 10 minutes' duration and trawl hauls of 15 minutes, except where stated.

Station Number	Date	Depth (metres)	Instrument used	
1	1. xi. 50	—	Large dredge	Test hauls just off Accra. Not on map.
2	1. xi. 50	—	" "	
3	1. xi. 50	—	" "	
5	9. xi. 50	13	" "	
6	9. xi. 50	12	" "	
8	12. xi. 50	13	" "	
9	12. xi. 50	13	" "	
10	19. xi. 50	14	" "	
11	19. xi. 50	13	" "	
12	19. xi. 50	16	" "	
14	28. xi. 50	20	" "	
15	28. xi. 50	—	" "	
16	28. xi. 50	17	" "	
17	28. xi. 50	12	" "	
18	28. xi. 50	—	" "	5 minutes
19	30. xi. 50	16	" "	
20	30. xi. 50	20	" "	
21	7. xii. 50	11	" "	
23	7. xii. 50	14	" "	
24	7. xii. 50	21	" "	
27	14. xii. 50	22	" "	5 minutes
28	14. xii. 50	30	" "	8 minutes
29	20. xii. 50	13	" "	
30	20. xii. 50	13	" "	
31	20. xii. 50	11	" "	
32	20. xii. 50	11	" "	
33	20. xii. 50	28	" "	
35	21. xii. 50	37	" "	30 minutes
45	31. xii. 50	35	" "	
47	4. i. 51	44	Small dredge	15 minutes
48	4. i. 51	44	Large dredge	
52	4. i. 51	45	Small dredge	
53	15. i. 51	11	" "	
54	15. i. 51	11	" "	
55	15. i. 51	12	" "	
56	15. i. 51	16	" "	
57	17. i. 51	16	" "	
58	17. i. 51	20	" "	
59	17. i. 51	24	" "	
61	18. i. 51	26	" "	
62	18. i. 51	30	" "	
63	18. i. 51	36	" "	
65	22. i. 51	7	" "	
66	22. i. 51	10	" "	

Station Number	Date	Depth (metres)	Instrument used	
67	22. i. 51	14	" "	
68	22. i. 51	19	" "	
69	22. i. 51	22	" "	
70	24. i. 51	25	" "	
71	24. i. 51	30	" "	
72	24. i. 51	38	" "	
73	24. i. 51	41	" "	
78	21. ii. 51	13	Agassiz trawl	
79	21. ii. 51	10	" "	
80	21. ii. 51	10	" "	
81	21. ii. 51	13	" "	
83	26. ii. 51	15	" "	30 minutes
84	26. ii. 51	—	" "	
85	26. ii. 51	21	" "	
86	28. ii. 51	—	" "	30 minutes
87	5. iii. 51	11	" "	
88	5. iii. 51	13	" "	
89	7. iii. 51	16	" "	
90	7. iii. 51	21	" "	
92	12. iii. 51	11	" "	
93	12. iii. 51	12	" "	
94	12. iii. 51	17	" "	
95	12. iii. 51	17	" "	30 minutes
96	12. iii. 51	—	" "	30 "
97	14. iii. 51	20	" "	
98	14. iii. 51	25	" "	
99	14. iii. 51	28	" "	
103	29. iii. 51	10	" "	30 minutes
104	29. iii. 51	13	" "	
105	29. iii. 51	17	" "	
106	29. iii. 51	19	" "	
107	30. iii. 51	23	" "	
108	30. iii. 51	29	" "	
110	4. iv. 51	40	" "	20 minutes
111	4. iv. 51	43	" "	
112	4. iv. 51	43	" "	
117	5. iv. 51	64	" "	30 minutes
121	11. iv. 51	8	" "	
122	11. iv. 51	8	" "	
123	11. iv. 51	9	" "	
124	12. iv. 51	11	" "	
125	12. iv. 51	16	" "	
126	12. iv. 51	20	" "	
127	14. iv. 51	17	" "	
129	26. iv. 51	26	" "	
130	26. iv. 51	32	" "	
131	2. v. 51	37	" "	
132	2. v. 51	44	" "	
133	2. v. 51	51	" "	

APPENDIX 3

List of occasional sources of specimens.

The Volta estuary. The Volta debauches into the sea some 60 miles east of Accra onto a sandy coastline. At its mouth the town of *Ada* has a marine

front with a pure sand beach fringed with coconut palms, while the river front is estuarine in character with a sticky mud shore with jetties and boat hulls. Three miles upriver is *Big Ada* with a beach of sandy mud and mud. Salinities are certainly high in the dry season but in flood there must be considerable dilution.

Higher still, 17 miles from Ada, lies *Tefle* near the limit of tidal influence. The shores are steep earth banks and the water is slightly saline even at low water of spring tides in the dry season. Below Tefle the area is riddled with tidal creeks, saline pools, and mangrove swamps, while eastwards lies the enormous Keta lagoon usually connected by channels (even if weed choked) with the Volta estuary. To the west lies the smaller, but still large, Songaw lagoon (not connected to the Volta) which dries out to a large extent in the dry season and leaves a glittering white sea of salt-covered mud.

At distances of 52 and 62 miles respectively from Ada, *Akuse* with rock-strewn rapids in the dry season, and *Senchi* with a very deep swift running channel and steep earth banks, provided a few specimens of freshwater fish, snails and prawns. Both fish and prawns are commercially fished as is the Volta " oyster " (*Egeria radiata*) in the region of Akuse.

Chorkor, Accra. West of the lighthouse at Accra, the Government Prisons fish a large seine net on a sand beach which brings in specimens from several metres depth. Numerous specimens were obtained from this source.

Ankobra Ferry, 157 miles west of Accra. Just inside the mouth of the Ankobra the beach is of sandy mud and various hulls and logs lie about.

Half Assini, 200 miles west of Accra. A little beyond Axim unbroken sand stretches for over 50 miles to the Ghana border at the Tano Lagoon. Half Assini is near the end of this stretch and a few specimens were obtained from the wreck of a stranded steel ship, whose Captain's grave lies in the town.

Kpeshi lagoon. A few specimens were obtained from this lagoon just beyond Labadi some five miles east of Accra.

Osu Fisheries. Specimens have been obtained from the trawls and dredges of the Government Fisheries boat.

Bottom net. Numerous specimens were obtained by the use of a *pra pra suadi*. This is a wide-meshed wall net about 100 yards long which is set on the bottom and hauled after 24 hours. The position of the net was not determined but the depth of water was sounded and it was always set just off Accra. It captured a few fish but also surprising numbers of box crab (*Calappa*), lobsters, spider crabs, hermit crabs, starfish, alcyonarian colonies and occasional molluscs.

APPENDIX 4

A list of the Mollusca (excluding Cephalopoda).

The names used are those in Nickles (1950) and Buchanan (1954, 1956) except where otherwise stated. An asterisk denotes a species or a record new to Buchanan's two lists. The number of specimens collected is given for each shore station but for sub-littoral stations the total number only is given. Only living specimens are recorded. I am indebted to Mr H. O. Ricketts of the British Museum of Natural History for much preliminary sorting of the

Station Number	Date	Depth (metres)	Instrument used	
67	22. i. 51	14	„	„
68	22. i. 51	19	„	„
69	22. i. 51	22	„	„
70	24. i. 51	25	„	„
71	24. i. 51	30	„	„
72	24. i. 51	38	„	„
73	24. i. 51	41	„	„
78	21. ii. 51	13	Agassiz trawl	
79	21. ii. 51	10	„	„
80	21. ii. 51	10	„	„
81	21. ii. 51	13	„	„
83	26. ii. 51	15	„	„ 30 minutes
84	26. ii. 51	—	„	„
85	26. ii. 51	21	„	„
86	28. ii. 51	—	„	„ 30 minutes
87	5. iii. 51	11	„	„
88	5. iii. 51	13	„	„
89	7. iii. 51	16	„	„
90	7. iii. 51	21	„	„
92	12. iii. 51	11	„	„
93	12. iii. 51	12	„	„
94	12. iii. 51	17	„	„
95	12. iii. 51	17	„	„ 30 minutes
96	12. iii. 51	—	„	„ 30 „
97	14. iii. 51	20	„	„
98	14. iii. 51	25	„	„
99	14. iii. 51	28	„	„
103	29. iii. 51	10	„	„ 30 minutes
104	29. iii. 51	13	„	„
105	29. iii. 51	17	„	„
106	29. iii. 51	19	„	„
107	30. iii. 51	23	„	„
108	30. iii. 51	29	„	„
110	4. iv. 51	40	„	„ 20 minutes
111	4. iv. 51	43	„	„
112	4. iv. 51	43	„	„
117	5. iv. 51	64	„	„ 30 minutes
121	11. iv. 51	8	„	„
122	11. iv. 51	8	„	„
123	11. iv. 51	9	„	„
124	12. iv. 51	11	„	„
125	12. iv. 51	16	„	„
126	12. iv. 51	20	„	„
127	14. iv. 51	17	„	„
129	26. iv. 51	26	„	„
130	26. iv. 51	32	„	„
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APPENDIX 4

A list of the Mollusca (excluding Cephalopoda).

The names used are those in Nickles (1950) and Buchanan (1954, 1956) except where otherwise stated. An asterisk denotes a species or a record new to Buchanan's two lists. The number of specimens collected is given for each shore station but for sub-littoral stations the total number only is given. Only living specimens are recorded. I am indebted to Mr H. O. Ricketts of the British Museum of Natural History for much preliminary sorting of the

collection and for some provisional identifications. The collection will be lodged at the British Museum of Natural History.

LORICATA

**Acanthochiton Adansoni* de Rochebrune
24 specimens, 9 stations (Nos. 35, 45, 48, 73, 110, 111, 112, 132, 133), 35–51 metres.

**Ischnochiton cessaci* de Rochebrune
2 specimens off Densu mouth, in 16 m.

Chiton canariensis d'Orbigny
Prampram 9, *Christiansborg 4, *Apam 2, *Prince's Town 3, Dixcove 1, Axim H.R. 26, L.H.R. 1.

GASTROPODA

Haliotis tuberculata L.
Dixcove common, Axim L.H.R. 1.

Diodora menkeana Dunker
Prampram 2, *Dixcove 2.

**Fissurella coarctata* King (?)
Christiansborg 1.

Fissurella nubecula L.
Prampram 80, Christiansborg 17, Winneba 30, *Apam 2, Dixcove 6, Axim H.R. 10, L.H.R. 11.

Patella safiana Lamarck
Christiansborg 1, Winneba 12, Apam 2, Sekondi 1, Dixcove 12.

Patella sp.
Apam, Prince's Town, Half Assini.

Calliostoma sp. (*granulatum* ?)
12 specimens, 6 stations (45, 110, 111, 112, 117, 132), 35–64 metres.

Clanculus kraussi Philippi
*Ningo 2, Prampram 12, Dixcove 1, *Axim H.R. 3, L.H.R. 6.

Clanculus guineensis Gmelin
Prampram 46, *Apam 1.

**Gibbula joubini* Dautzenberg (?)
Prampram 9, Dixcove 1.

Tricolia pullus (L.)
Prampram 125, *Christiansborg 18, *Apam 1, *Axim L.H.R. 2.

Nerita senegalensis Gmelin
Prampram 12, Christiansborg 2, Winneba 25, Apam 6, Sekondi 10, Prince's Town 40, Axim L.H.R. 12, H.R. 40.

Littorina angulifera (Lamarck)
Ada (Volta estuary), H.W.M. hundreds.

Littorina punctata Gmelin
Christiansborg 50, Winneba hundreds, Sekondi hundreds, Prince's Town 9, Dixcove 7, Axim H.R. 11, east side of bay 20, Half Assini 2.

Littorina cingulifera Dunker
Sekondi 4, Half Assini 14.

Tectarius granosus Philippi
*Winneba 2, *Prince's Town 40, Axim H.R. 1, east side of bay 30.

Turritella annulata Kiener
Many thousands, 45 stations (Nos. 9, 10, 11, 12, 14, 15, 16, 20, 23, 24, 27, 28, 33, 57, 58, 59, 61, 62, 63, 67, 68, 69, 72, 80, 81, 86, 88, 90, 92, 94, 95, 96, 97, 98, 99, 106, 117, 125, 126, 127, 129, 130, 131, 132, 133), 10–64 metres.

**Turritella torulosa* Kiener
Christiansborg 1, Axim H.R. 2.

Turritella bicingulata Lamarck
Prampram 3.

**Solarium granulatum* Lamarck (?)
2 sp. St. 131 and 133, 37–51 metres. Prampram 2.

Dendropoma ghanaense Keen & Morton (1960)
Dixcove hundreds (as *Vermetus* sp. in Buchanan, 1954).

Tenegodus senegalensis Recluz
*Axim L.H.R. 1.

Planaxis lineatus (da Costa)
Prampram 12, *Prince's Town 70, *Axim L.H.R. 10, H.R. 20.

Tympanotus fuscatus and *T.f.* var. *radula* (L.)
Big Ada (Volta estuary) and adjacent creeks dozens, Kpeshi lagoon, Labadi (near Accra) 20.

Alaba cullicreti Dautzenberg
Prampram (Reef No. 2), dozens.

**Cerithium guinaicum* Philippi
Dixcove 1.

Cerithium atratum Born
Prampram 340, *Sekondi 2, Axim L.H.R. 8.

Triphora perversa L.
*2 sp. St. 47, at 44 metres.

Opalia crenata L.
*Christiansborg 1.

Janthina fragilis Lamarck
Teshi 3.

Niso chevreuxi Dautzenberg
2 sp. Sts. 67 and 111, *14 and 43 metres.

Calyptraea chinensis L.
40 specimens, 15 stations (Nos. 1, 8, 17, 19, 21, 29, 30, 53, 55, 67, 70, 81, 88, bottom net, and 2 miles west of Densu mouth), mostly 11–16 metres, a few down to 48 metres.

Crepidula porcellana Lamarck
var. *jenae*
*Ningo 1, Prampram 12, *Apam 4, Dixcove 7, Axim H.R. 2, L.H.R. 1.
var. *garnot*
8 specimens, 5 stations (83, 84, 130, 133, and 2 miles west of Densu), 15–32 metres. Of these one had some characters of var. *aculeata*, one those of var. *sulin*, and one those of var. *jenac*, but all were nearer to var. *garnot* except for the Densu specimen which could be var. *jenac*.

Xenophora senegalensis (P. Fischer)
90 specimens, 7 stations (nos. 45, 110, 111, 112, 117, 132, 133), 35–64 metres.

Apporhais senegalensis Gray
29 specimens, 5 stations (Nos. 111, 112, 130, 131, 132), 37–51 metres.

Strombus bubonius Lamarck
5 specimens, St. 130 and 2 miles west of Densu, 16–32 metres.

Strombus sp.
1 specimen, St. 133, 51 metres.

**Natica fulminea* Gmelin
2 specimens, Stations 33 and 61, 26–28 metres.

Natica fanel (Adanson)
Prampram 1, Christiansborg 1 (both small and identity uncertain). 7 specimens, Stations 112, 117, 130, 132, 32–64 metres.

Natica fanel var. *rocquignyi* E. Fischer
18 specimens, 10 stations (Nos. 20, 24, 27, 28, 58, 61, 68, 69, 97), 19–30 metres.

**Natica gruveli* Dautzenberg
Apam 1.

Natica marochiensis (Gmelin)
Apam 1 ; 3 specimens Stations 45, 111, 35–43 metres.

**Sigaretus concavus* Lamarck
2 specimens, Stations 45 and 71, 30–35 metres.

Cypraea stercoraria L.
Prampram 1, Christiansborg 3.

Cypraea lurida (L.)
Prampram 2, Dixcove 6, *Axim L.H.R. 5.

**Cymatium trigonum* Gmelin
2 specimens, Station 132, 44 metres.

Distortrix ridens Reeve
10 specimens, 6 stations (Nos. 33, 94, 129, 130, 131, 133), *17–37 metres.

**Bursa pustulosa* Reeve
8 specimens, 5 stations (Nos. 47, 112, 117, 132, 133), 43–64 metres.

Murex cornutus L.
6 specimens, 6 stations (Nos. 89, 110, 117, 131, 133 and Chorkor seine net) 2 or 3—64 metres.

Murex bourgeoisi Tournouër
*Axim H.R. 1, *over 100 specimens, 7 stations (Nos. 106, 127, 129, 130, 133, off Christiansborg and Chorkor seine) L.W.M.—51 metres. (Abundant at Stations 129 and 130 in 26–30 metres.)

Murex angularis lyrata Adams (?)
5 specimens, Stations 129, 130, 133. *26–51 metres.

Drupa nodulosa C. B. Adams
Prampram 23, *Apam 1, Dixcove 1, *Prince's Town 1, *Axim H.R. 14, L.H.R. 14.

Thais haemastoma L.
Prampram 6, Christiansborg 40, Winneba 211, Apam 5, Sekondi 2, Axim H.R. 5 (one doubtful specimen from 13 metres off Accra).

Thais nodosa L.
Prampram 11, Christiansborg 1, *Winneba 1, *Apam 4, Dixcove 1, *Axim H.R. 1, L.H.R. 1.

Tritonalia fasciata Sowerby
*Axim H.R. 2, *St. 79 1 in 10 metres.

Coralliophila meyendorffi (Calcara)
4 specimens, Sts. 62, 131, 30–37 metres.

Columbella rustica (L.) var. *striata* Duclos
Prampram 43, *Winneba 3, Dixcove 8, *Axim H.R. 2, L.H.R. 1.

Phos grateloupianus Petit de la Saussaye
11 specimens, 7 stations (63, 111, 112, 117, 130, 132, 133), 32–64 metres.

Cantharus viverratus (Kiener)
*Ningo 1, Prampram 8, *Christiansborg 2, *Winneba 1, *Apam 1, *Prince's Town 1, Dixcove 2, Axim L.H.R. 2, H.R. 7.

Semifusus morio L.
Prampram 3, Christiansborg 4, *Apam 1, *Axim H.R. 1.

Nassa obliqua Kiener
1 specimen, Station 130, 32 metres.

Nassa incrassata Ström var. *sengalensis* von Maltzan
25 specimens, 5 stations (Nos. 110, 130, 131, 132, 133), 32–57 metres.

**Nassa argentea* Marrat
6 specimens, 4 stations (Nos. 54, 68, 92, 104), 11–19 metres.

Nassa tritoniformis Kiener
7 specimens, 6 stations (Nos. 58, 61, 67, 78, 97, 99), 13–28 metres.

Nassa trifasciata A. Adams
1 specimen, Station 28, 30 metres.

Lathyrus filosus Schubert and Wagner
80 specimens, 11 stations (Nos. 47, 62, 98, 110, 111, 112, 129, 130, 131, 132, 133), 26–44 metres. (Station 130 had 36 specimens in 32 metres.)

Olivancillaria hiatula Gmelin
*Christiansborg 6, *Apam 12, Chorkor Seine 2, bottom net off Accra 1, in 13 metres. (L.W.M. –13m.)

**Oliva flammulata* Lamarck
2 specimens, Stations 61 and 126, 20–26 metres.
Oliva acuminata Lamarck
*1 specimen, Station 126, 20 metres.
Oliva annotata Marrat
1 specimen, Station 122, 8 metres.
Mitra scrobiculata (Brocchi)
1 specimen, Station 112, 43 metres.
Mitra fusca Swainson
*Winneba 1.
**Mitra hamillei* Lamarck
4 specimens, Stations 57 and 93, 12–16 metres.
**Mitra carinata* Swainson
1 specimen, Station 28, 30 metres.
Cymbium porcinum Lamarck
3 specimens, Chorkor Seine and bottom net, to 14 metres.
Cymbium gracile Broderip
1 specimen, bottom net off Accra, 14 metres.
Cancellaria cancellata (L.)
190 specimens, 18 stations (Nos. 11, 16, 23, 27, 33, 61, 62, 78, 89, 90, 98, 99, 111, 112, 126, 130, 131, 132), 13–44 metres. (120 specimens from Station 130 in 32 metres, 18 from Station 89 in 16 metres, and 17 from Station 99 in 28 metres.)
Marginella olivaeformis Kiener
3 specimens, Stations 117 and 131, 37–64 metres.
Clavatula lelieuri (Recluz) (Knudsen, 1952)
About 15 specimens, 8 stations (Nos. 27, 33, 67, 89, 97, 130, 131, 133), 14–51 metres.
Clavatula nifat (Adanson)
*19 specimens, 6 stations (Nos. 97, 130, 131, 133, bottom net off Accra and Chorkor seine), 2 or 3–51 metres (15 from 32–37 metres).
Clavatula diadema Kiener
3 specimens, Stations 117 and 130, 32–64 metres.
**Clavatula aculeiformis* Lamarck
2 specimens, Station 67, 14 metres.
Clavatula milleti Petit de la Saussaye
1 specimen, Station 58, 20 metres.
Clavatula lineata Lamarck
1 specimen, Station 68, 19 metres.
**Clavatula coerulea* Weinkauff
5 specimens, Stations 67 and 68, 14–19 metres.
Clavatula gabonensis J. C. Melvill (Knudsen, 1952)
15 specimens, 7 stations (Nos. 73, 110, 111, 112, 130, 132, 133), 32–51 metres.
Turris undatiruga Bivona
*18 specimens, 7 stations (Nos. 110, 111, 112, 130, 131, 132, 133), 32–51 metres.
Drillia rosacea (Reeve) (Knudsen, 1952)
10 specimens, 6 stations (Nos. 112, 117, 130, 131, 132, 133), 32–64 metres.
Turris carbonaria Reeve
*11 specimens, 7 stations (Nos. 57, 89, 99, 110, 130, 131, 133), 16–51 metres.
Turris sp. near *carbonaria*
2 specimens, Station 130, 32 metres.
Turris sp. probably *Turris torta* (Dautzenberg) (Knudsen, 1952)
3 specimens, Stations 130 and 131, 32–37 metres.
Asthenotoma spiralis (E. A. Smith) (Knudsen, 1952)
2 specimens, Stations 67 and 132, 14–44 metres.
Genota mitraeformis Wood
9 specimens, 6 stations (Nos. 110, 111, 112, 130, 131, 132), 32–44 metres.
**Conus papilionaceous* Hwass
2 specimens, Chorkor seine.

Conus ambiguus Reeve
1 specimen, Station 132, 44 metres.
Conus genuanus Hwass
1 specimen, Station 132, 44 metres.
Terebra grayi E. A. Smith (Knudsen, 1952)
9 specimens, 7 stations (Nos. 16, 24, 27, 59, 67, 68, 69), 14–24 metres.
Terebra micans Hinds
Labadi (just east of Accra), 24, Accra harbour 1, Apam 2. Near L.W.M.
Terebra sp.
Apam 1.
**Actaeon tornatilis* L.
3 specimens, Stations 54, 67, and west of Densu mouth, 11–16 metres.
Acteocina knockeri E. A. Smith
Prampram 2.
Haminea orbignyana Férussac
Prampram 1, Christiansborg 1, Apam 1.
Philine aperta L.
6 specimens, Stations 35 and 117, 37–64 metres.
**Aplysia dactylomela* Rang (Eales, 1957)
9 specimens.
**Aplysia juliana* Quoy and Gaimard (Eales, 1957)
1 specimen.
**Aplysia fasciata* Poiret (Eales, 1957)
2 specimens.
**Aplysia winneba* Eales (Eales, 1957)
59 specimens, Prampram, Christiansborg, Winneba, Apam, Dixcove, Axim H.R., Chorkor seine and dredge off Accra.
Siphonaria pectinata (L.)
Prampram hundreds, Christiansborg 12, Winneba dozens, Apam 12, Sekondi dozens, Axim H.R. dozens, L.H.R. not so abundant, Half Assini 3.

SCAPHOPODA

Dentalium coarti Dautzenberg
3 specimens, Stations 9, 55 and 67, 12–14 metres.

LAMELLIBRANCHIATA

Leda bicuspidata Gould
3 specimens, Stations 33 and 68, 19–28 metres.
Leda rostrata Montagu
2 specimens, Stations 2 and 33, 28 metres.
Arca noe L.
25 specimens, including one 45 mm. long, 9 stations (Nos. 47, 48, 110, 117, 130, 131, 132, 133, and west of Densu mouth), 32–64 metres (18 at 44 metres). And one from Apam.
Arca subglobosa (Dunker)
95 specimens (mostly small but largest one 30 mm. long), 11 stations (Nos. 45, 53, 54, 55, 65, 66, 69, 126, 131, 133, and Chorkor seine), 7–51 metres (80 specimens were small and came from Stations 54 and 66 in 10 and 11 metres).
Arca afra Gmelin
Prampram 3, *Prince's Town 4, Dixcove 4, *Axim L.H.R. 2. (One from Prampram and the Dixcove specimens are doubtful.)
Arca geissi (Dunker) Kobelt (?)
Prince's Town 4, Dixcove 2, Axim H.R. 2, L.H.R. 2.
Arca gambiensis Reeve
Axim L.H.R. 1, and two from beyond the Densu mouth in 16 metres.
**Arca A*
Prampram 1, Christiansborg 1, Apam 6, Axim H.R. 3, L.H.R. 2.

**Arca B*
Axim H.R. 2.

**Arca* spp.
Axim L.H.R. 1, off Densu and Station 53, 2 in 11 and 16 metres.

Modiolus lulat (Adanson)
6 specimens, 3 stations (Nos. 117, 132, 133), 44–64 metres.

Modiolus stultorum Jousseaume
10 specimens, 6 stations (Nos. 11, 12, 32, 53, 55, 65), 11–16 metres.

Brachyodontes puniceus Gmelin
*Winneba 9, *Sekondi 1, *Prince's Town 24, Dixcove 10, Axim H.R. 25, L.H.R. 8. Also 3 from mangroves in the Densu estuary.

**Brachyodontes niger* Gmelin
Christiansborg 23, Winneba 7, Sekondi 2, Axim H.R. 4, Ankobra ferry 1 (upper shore and splash zone). Also one from Station 45 in 35 metres.

**Modiolaria* sp.
Mangroves in Densu estuary 2.

Modiolaria barbatella Cantraine
*Bottom net in 14 metres 2, *Station 117 in 64 metres 1, *Winneba 1, *Apam 1, *Sekondi 2, Axim H.R. 3.

Lithophaga lithophaga L.
Axim L.H.R. 1, H.R. 1.

Lithophaga aristata (Solander)
*Winneba 6, *Sekondi a few, *Prince's Town 1, Dixcove 40, Axim L.H.R. 1, Half Assini 3.

Mytilus perna L.
Christiansborg 6, Chorkor seine dozens, Winneba 60, Apam 1, Sekondi 1, Prince's Town 2, Axim H.R. 15, Half Assini 40.

Pedalion perna L.
Prampram 3, *Apam 4, *Sekondi 12, *Prince's Town 3, Dixcove 1, Axim H.R. 18, L.H.R. 13.

Pteria hirundo (L.)
2 specimens, Station 117, 64 metres.

Pteria atlantica Lamarck
20 specimens on sea fans, Chorkor seine and off the Densu mouth down to 16 metres.

Pinna rudis (L.)
Christiansborg 1, *Axim H.R. 1, L.H.R. 2. Up to 14 cm. long.

Pecten exoticus Chemnitz
63 specimens, 18 stations (Nos. 5, 6, 30, 32, 53, 67, 81, 93, 102, 103, 122, 123, bottom net five times, off Densu mouth), 8–16 metres, with one at 40 metres.

Pecten sp.
1 specimen, Station 117, 64 metres.

Anomia ephippium L.
*Prince's Town 2, *Axim H.R. 2, L.H.R. 1.

Ostrea cucullata Born (?)
*Prampram 2, *Dixcove 1, *Axim H.R. 12, L.H.R. 1, *off Densu mouth at 16 metres 1 (all ascribed to this species with some doubt).

**Ostrea denticulata* Born
Sekondi 6, Half Assini 12, Axim ? 1.

Ostrea tulipa Lamarck
Dozens on *Tympanotus* at Big Ada (Volta Estuary); on piers and beached hulls at Ada (Volta Estuary) and at the Ankobra ferry; and in the Chorkor seine. *Also on rocks at H.W.M. Christiansborg, and Winneba.

**Ostrea hyotis* L.
4 specimens, Station 47, 44 metres.

Ostrea folium L.
3 specimens, Station 48 at 44 metres, beyond Densu mouth in 16 metres, and on sea fan (origin unrecorded).

**Ostrea* sp.
3 specimens, Station 133, 51 metres. Axim H.R. 1.

Crassatella triquetra Reeve
10 specimens, 5 stations (Nos. 47, 111, 117, 131, 132, 133), 37–64 metres.

**Crassatella divaricata* (Chemnitz)
Axim H.R. 1.

Cardita lacunosa Reeve
16 specimens, 6 Stations (Nos. 47, 48, 73, 117, 133, and beyond Densu mouth) *41–64 metres (except the Densu specimens in 16 metres).

Beguina senegalensis Reeve
Prampram 6, *Christiansborg 1, *Prince's Town 5, *Axim H.R. 15, L.H.R. 5.

Dreissena africana van Beneden
Mangroves in Densu estuary, 1.

**Diplodonta diaphana* Gmelin
Prampram 1, Apam 1, Dixcove 1, Axim H.R. 2, bottom net of Chorkor in 14 metres 1.

Kellya rubra (Montagu) (?)
Prampram 4, Prince's Town 1.

Galeomma turtoni Sowerby
*Ningo 1, Prampram 29.

Chama gryphina Lamarck
Winneba 1. Also 1 from Station 48 in 44 metres, but doubtful determination.

Chama crenulata Lamarck
Prampram 7. *Also 9 specimens from beyond Densu mouth in 16 or more metres and three others which could be this species from Stations 126 and 133, 20–51 metres.

Cardium ringens Gmelin
30 specimens, Stations Nos. 1, 5, 11, 21, 30, 32, 54, 55, 92, 11–13 metres.

**Cardium costatum* L.
3 large specimens, Chorkor seine, below L.W.M.

Cardium kobelti von Maltzan
16 specimens, Stations 117, 132, 133, 44–64 metres.

**Cardium* sp.
1 specimen, Station 117, 64 metres. 3 specimens, Station 103, 10 metres.

Tivela tripla L.
Christiansborg 13, Chorkor seine 3.

**Dosinia lupinus* L.
49 specimens, 17 stations (Nos. 5, 32, 48, 52, 53, 54, 55, 65, 66, 67, 68, 72, 111, 117, 123, 124, 133), 7–64 metres (but none between 19–37).

Venus punctigera (Dautzenberg)
1 specimen, Station 117, 64 metres.

Petricola pholadiformis Lamarck
Prampram 4, Chorkor seine 1.

**Mactra glabrata* L.
1 specimen from beyond Densu mouth, about 16 metres.

Mactra nitida Spengler
16 specimens, 6 stations (Nos. 27, 33, 59, 68, 69, 70), 19–28 metres.

Donax rugosus L.
Prampram 46, Accra harbour dozens.

Donax pulchellus Hanley
Christiansborg and Apam, in thousands.

Donax acutangulus Deshayes
1 specimen, Station 121, 8 metres.

**Gastrana matadoa* (Adanson) Gmelin
Axim L.H.R. 1.

Tellina compressa Brocchi
7 specimens, 6 stations (Nos. 24, 33, 58, 90, 97, 126), 20–28 metres.

**Tellina planata* L.
Axim L.H.R. 1.

Cultellus tenuis Gray
11 specimens, 6 stations (Nos. 28, 32, 33, 59, 65, 68), 7–30 metres.

**Solen guineensis* Gray
Chorkor seine 1.

**Saxicava arctica* L.
Prampram 1, Sekondi 1, Prince's Town 1, Axim H.R. 1. Also 2 specimens at Station 133, in 51 metres, and one on a sea fan (unrecorded locality).

Aloidis striata (E. A. Smith)
Prampram 9, Apam 1, Prince's Town 1, Dixcove 4, Axim L.H.R. 2, H.R. 3. Also Chorkor seine 1.

**Aloidis gibba* Olivi
2 specimens, Stations 48, 117, 44–64 metres.

Aloidis dautzenbergi Lamy
2 specimens, Stations 33 and 70, 25–28 metres.

Teredo pedicellata de Quatrefages
Bottom net off Chorkor in 14 metres.

APPENDIX 5

List of fishes

The collection of more than 1,000 specimens does not represent an intensive investigation of the fish fauna. All specimens taken at the shore collecting stations and in the dredges and trawls of the sub-littoral survey are included and to these have been added a large number of specimens from the Prisons Department's seine net at Chorkor and occasional brackish and freshwater fish wherever obtained. The collection has been determined by Dr. J. Cadenet, Chief of the Biology Section of the Institut Francais d'Afrique Noire at Gorée, Sénégal, and has been compared with the account given by Irvine (1947). Page references are given where the species is described by Irvine and otherwise the species is recorded as new for Ghana. Of the 140 species listed, many constitute new locality records, while 54 species are new to Ghana and include three new species.

SELACHII

Scoliodon terrae novae (Richardson). Chorkor seine, 1. (Irvine, p. 88.)

Rhinobatus albomaculatus Norman. Chorkor seine, 4. (Irvine, p. 94.)

Torpedo torpedo (L.) Chorkor seine, 1 ; Station 130 in 32 metres, 1. (New record.)

Tetronarce sp. 8 Chorkor seine (this is the species figured in Irvine as *Torpedo nobiliana* (p. 92)).

Dasyatis (*Trigon*) *margarita* (Gunther). Chorkor seine, 2 (one a foetus) ; bottom net, 1 in 11 metres, 2 in 13 metres, 2 in 18 metres. (Irvine, p. 99, as *Trygon*.)

TELEOSTEI

Megalops atlanticus C.V. Kpeshi lagoon, 1. (Irvine, p. 106.)

Engraulis probably *E. encrasicolus* (L.). Chorkor seine, 4. (Irvine, p. 112.)

Ethmalosa dorsalis (Dumeril). Chorkor seine, 4 ; Kpeshi lagoon 1. (Irvine, p. 110.)

Sardinella aurita Val. Chorkor seine, Feb., Mar., May, Dec., 8. (Irvine, p. 109.)

Sardinella cameronensis Regan. Chorkor seine, Feb., Mar., May, Dec., 12. (Irvine, p. 109.)

Harengula rouxi Poll. 1953. Chorkor seine, Mar., May, Oct., 5. (New record.)

Pellona africana (Bloch). Chorkor seine, Mar., May, Oct., 10. (Apparently the *Ilisha melanota* of Irvine, p. 111.)

Trachinocephalus myops (Schneider). Bottom net in 18 metres, 1. (Irvine, p. 112.)

Saurida parri Norman. 6 specimens, 37–64 metres. (New record.)
Fodiator acutus (C.V.). Chorkor seine, 3. (New record.)
Ablennes hians (C.V.). Chorkor seine, 1. (Irvine, p. 119.)
Hemiramphus brasiliensis (L.). Chorkor seine, 4. (Irvine, p. 121.)
Hyporamphus schlegili (Bleeker). Chorkor seine, 1. (Irvine, p. 120, as *H. calabaricus*.)
Conger macrops Gunther. Near Teshi, 1. (New record.)
Caecula (*Sphagebranchus*) *cephalopeltis* (Bleeker). No locality, 1. (Irvine, p. 119.)
Pisodonophis semicinctus (Richardson). Chorkor seine, 2. (Irvine, p. 118, as *Ophichthus*.)
Mystriophis rostellatus (Richardson). Near Teshi, 2. (New record.)
Lycodontis vicinus (Castelnau). Chorkor seine, 1; Prampram shore, 3; Christiansborg, 1. (Irvine, p. 116, as *Gymnothorax*.)
Muraenophis robusta (Osorio). Prampram, 1. (New record.)
Arius (*Trachysurus*) *heudeloti* C.V. Chorkor seine, 2. (New record.)
Chrysichthys nigrodigitatus (Lacep.). Ankobra Ferry, 1. (Irvine, p. 246.)
Clarias senegalensis C. & V. Pool near Big Ada, 5. (Irvine, p. 255.)
Psettodes belcheri Bennett. Chorkor seine, 2; bottom net in 13 metres, 1. (Irvine, p. 206.)
Arnoglossus imperialis (Rafinesque). Station 117 in 64 metres, 1. (New record.)
Arnoglossus sp. near *A. capensis* Boulenger. Stations Nos. 110, 117, 131, 37–64 metres, 10. (New record.)
Eucitharus linguatula (L.). Locality uncertain. Believed in 14 and 16 metres off Accra, 5. (New record.)
Platophrys (*Bothus*) *podas* (Delar.). Stations Nos. 83, 85, 86, 88, 89, 94, 105, 127, 132, 13–44 metres, 26. (New record.)
Synacium micrurum Ranzani (= *Hemirhombus guineensis*). Stations Nos. 78, 85, 86, 89, 94, 105, 107, 112, 131, 132, 13–44 metres, 38. (Irvine, p. 207.)
Citharichthys stampflii (Steind). Stations Nos. 67, 123, 9–14 metres. Also Chorkor seine, Kpeshi lagoon, Ada (Volta estuary), 10. (Irvine, p. 208.)
Synaptura lusitanica Capello. Chorkor seine, 1. (Irvine, p. 209.)
Heteromycteris proboscideus (Chab.). Station 35, 37 metres, 1. (New record.)
Monochirus hispidus Rafinesque. Station 112, 43 metres, 1. (New record.)
Microchirus boscanion (Chab.). Station 117, 64 metres, 2. (New record.)
Microchirus pseudocellatus sp. nov. Station 131, 37 metres, 1. (Was sent to Dr. Chabanaud but has not been described.)
Solea (*Pagusa*) *lascaris* (Risso). Stations 125, 131, and Chorkor seine, L.W.M. to 37 metres, 5. (New record.)
Bregmaceros macclellandi Thompson (?). Stations 57, 131, 16–37 metres, 2. The two specimens were badly preserved and could be *B. atlanticus* Goode & Bean 1895. (New record.)
Holocentrus hastatus C.V. (?). Dixcove, 1 juvenile. Determination doubtful. (Irvine, p. 124.)
Hippocampus sp. Station 117, 64 metres, 1. (Irvine, p. 123.)
Sphyraena guachancho C.V. Chorkor seine, 10. (Irvine, p. 196.)
Mugil (*Liza*) *falcipinnis* C.V. Kpeshi lagoon, 3. (Irvine, p. 199.)
Mugil bananensis Pellegrin. Ankobra ferry, 1. (New record.)
Pentanemus quinquarius (L.). Chorkor seine, 1. (Irvine, p. 201.)
Galeoides decadactylus (Bloch). Chorkor seine, Volta estuary (Ada), Christiansborg, 15. (Irvine, p. 202.)
Scomber colias Lowe. Chorkor seine, 1. (Irvine, p. 184.)
Cybium tritor C.V. Chorkor seine, 9. (Irvine, p. 186, as *Scomberomorus*.)
Trichiurus lepturus L. Chorkor seine, 1. (Irvine, p. 182.)
Stromateus fiatola L. Chorkor seine, 1. (Irvine, p. 195.)
Stromateus fasciatus L. Chorkor seine and near Teshi, 13. (New record.)
Decapterus punctatus (Agassiz). Chorkor seine, 1. (New record.)
Selar crumenophthalmus (Bloch). Chorkor seine, 6. (New record.)
Caranx ronchus Geof. St. Hilaire. Chorkor seine and Station 127 in 17 metres, 7. (Irvine, p. 138, as *Decapterus*.)
Caranx crysos (Mitch.). Chorkor seine, 2. (Irvine, p. 140.)
Caranx senegallus C.V. Chorkor seine, 3. (Irvine, p. 139, as *C. africanus*.)

Scyris (Caranx) alexandrinus (Geof. St. Hilaire). Chorkor seine, 13. (Irvine, p. 141.)
Argyreiosus setipinnis Gunther. Chorkor seine, 13. (Irvine, p. 142, as *Vomer setapinnis*.)
Chloroscombrus (Micropteryx) chrysurus (L.). Chorkor seine, 28. (Irvine, p. 143.)
Hemicaranx bicolor (Günther). Chorkor seine, 2. (Irvine, p. 138.)
Caesiomorus glaucus (L.). Chorkor seine and Christiansborg, 5. (Irvine, p. 144, as *Trachinotus*.)
Trachinotus goreensis C.V. Chorkor seine, 3. (Irvine, p. 145.)
Caranx carangus C.V. Volta estuary (Ada), 2. (New record.)
Caranx hippos (L.). Chorkor seine, 3. (Irvine, p. 140.)
Rachycentron canadum (L.) (= *Elacate nigra*). Chorkor seine, 1. (New record.)
Parakuhlia boulengeri Pellegrin. Christiansborg, 4. (Irvine, p. 152.)
Epinephelus aeneus (Geof. St. Hilaire). Chorkor seine, 4 ; Station 131, 37 metres, 2. (Irvine, p. 129,)
Epinephelus caninus Valenciennes 1843. Chorkor seine, 1. (New record.)
Cephalopholis (Epinephelus) nigri (Gunther). Ningo and Axim (Hospital reef), 3. (Irvine, p. 126, as *Petrometopon*.)
Paracentropristis heterurus Cadenat. Axim, Dixcove, Stations 117 and 131, 37–64 metres, 5. (New record.)
Priacanthus arenatus C.V. Off Accra, 4. (Irvine, p. 134.)
Rypticus saponaceus (Schneider). Chorkor seine, 2. (Irvine, p. 133.)
Lutjanus dentatus Dumeril. Creek of the Volta on the Big Ada road, 1. (New record.)
Brachydeuterus (Otoperca) auritus (C. & V.). Chorkor seine and off Accra, 26. (Irvine, p. 154.)
Pomadasys jubelini C.V. Chorkor seine, Volta estuary (Ada), Ankobra ferry, 8. (Irvine, p. 153.)
Dentex canariensis Steindachner. Chorkor seine and off Accra, 18 metres, 3. (New record.)
Pagrus ehrenbergi C.V. Chorkor seine, 2. (Irvine, p. 165.)
Pagellus sp. near *P. erythrinus* (L.). Chorkor seine, 4. (New record.)
Lethrinus atlanticus C.V. Chorkor seine, 1. (Irvine, p. 162.)
Box (Boops) boops (L.). Chorkor seine, 3. (Irvine, p. 165.)
Gerres melanopterus Bleeker. Chorkor seine and Kpeshi lagoon, 2. (Irvine, p. 151.)
Upeneus prayensis C.V. Chorkor seine, Stations 83, 86, in 15 metres. (Irvine, p. 161.)
Umbrina canariensis Val. Chorkor seine, 1. (Irvine, p. 160.)
Otolithus senegalensis C.V. Chorkor seine, 1. (Irvine, p. 156, as *Cynoscion senegalla*.)
Otolithus macrognathus (Bleeker). Chorkor seine, 2. (Irvine, p. 157, as *Cynoscion*.)
Larimus peli Bleeker. Chorkor seine, 1. (Irvine, p. 157.)
Drepane africana Osorio. Chorkor seine, 7. (*D. punctata*—Irvine, p. 181, is Indo-Pacific.)
Chaetodon luciae Rochebrune. Chorkor seine and Osu trawl, 4. (New record.)
Acanthurus monroviae Steindachner. Christiansborg, Dixcove, 4. (Irvine, p. 181, as *Teuthis*.)
Scorpaena angolensis Norman. Christiansborg, Station 127 in 17 metres, 2. (New record.)
Scorpaena scrofa L. Station 105 in 17 metres, 1. (Irvine, p. 203.) This specimen seems to be a new variety of the type.
Scorpaena senegalensis Steindachner. Chorkor seine, Axim, 2. (Irvine, p. 204.)
Scorpaena sp. Axim, 1. Probably a new species or related genus but too young to justify naming.
Trigla gabonensis Poll. et Roux 1955. Chorkor seine, 9. Probably the *T. hirundo* of Irvine, p. 205, but not *T. hirundo* L.
Lepidotrigla cadmani Regan. Station 132 in 44 metres, 1. (New record.)
Dactylopterus (Cephalocanthus) volitans (L.). Chorkor seine, 151, and bottom net in 18 metres, 2. (Irvine, p. 205.)
Platycephalus gruveli Pellegrin. Stations Nos. 85, 86, 105, 110, 111, 112, 117, 130, 131 ; Chorkor seine and bottom net, 13–64 metres, 33. (New record.)
Tilapia heudeloti Dumeril. Ankobra Ferry and Kpeshi lagoon, 3. (Irvine, p. 275.)
Tilapia zillii (Gervais). Creek of Volta estuary, 11. (Irvine, p. 273.)
Tilapia discolor Gunther. Lake Bosumtwi, 1. (Irvine, p. 274.)
Abudefduf analogus (Gill). Christiansborg, Axim, 20. (New record.)
Abudefduf marginatus (Bloch). Axim, 29. (Irvine, p. 174, as *Glyphisodon saxatilis* (L.).)
Pomacentrus leucostictus Müller Troschell. Prampram, Dixcove, Axim, 26. (New record.)

Thalassoma pavo (L.). Ningo, Dixcove, Axim, 7. (Irvine, p. 176, New record.)
Pseudoscarus hoefleri Steindachner. Dixcove, 1. (Irvine, p. 178, as *Callyodon*.)
Sparisoma cretense L. Ningo, 5. (New record.)
Electris lebretonis Steindachner. Dixcove, 2; Mangrove swamp Volta estuary, Ada, 25. (Irvine, p. 277.)
Periophthalmus koelreuteri (Pallas). Volta estuary and mangrove swamp, Ada and pool at Big Ada crossroads, 6. (Irvine, p. 191.)
Gobioides africanus (Giltay). Chorkor seine, 1. (New record.)
Oxyurichthys occidentalis (Bouleng.). Chorkor seine, 1. (New record.)
Gobius casamancus Rochebrune. Sekondi, 1; Axim, 29. (New record.)
Gobius soporator Valenciennes. Accra and bottom net in 16 metres, 4. (New record.)
Nematogobius ansorgei (Boulenger). Apam, Dixcove, Axim, 7. (Irvine, p. 192, as *Goboides* (?).)
Nematogobius brachynemus Pfaff. Prampram, Axim, 5. (New record.)
Gobioncillus sp. Stations 68 and 69, 19–22 metres, 5. Badly preserved and unidentifiable beyond the genus.
Echeneis naucrates L. Chorkor seine, 10. (Irvine, p. 211.)
Echeneis (*Remora*) *remora* L. Chorkor seine, 1. (New record.)
Trachinus radiatus Cuv. Bottom net, 18 metres, 1. (Irvine, p. 179.)
Uranoscopus polli Cadenat. Mouth of Densu and near Teshi, 2. (Irvine's figure, p. 181, is probably of this species and not *U. scaber*.)
Clinus (*Labrisomus*) *nuchipinnis* Quoy et Gaimard. Prampram, Christiansborg, Axim, 6. (Irvine, p. 193.)
Blennius crinitus Steindachner. Ningo, Christiansborg, Dixcove, Axim, 109. (New record.)
Rupiscartes atlanticus (C.V.). Christiansborg, Axim, 2. (New record.)
Salarias vomerinus C.V. Axim, 3. (New record.)
Batrachus (*Holobatrachus*) *didactylus* Schneider. Prampram, Chorkor seine, Station 131, in 37 metres, 3. (Irvine, p. 220.)
Batrachus (*Batrachoides*) *liberiensis* Steindachner. Prampram, Chorkor seine, 4. (Irvine, p. 219.)
Lecanogaster chrysea Briggs nov. gen. et sp. Ningo, 3. (New record—see next species.)
Opeatogenys cadenati Briggs n.sp. Ningo, 3. (New record.) The above two species were described by Briggs, J. C. in *Copeia* No. 3, 1957, p. 204–208, and the types lodged at the British Museum (Nat. Hist.).
Balistes forcipatus Gmelin. Chorkor seine, 1. (Irvine, p. 213.)
Aluterus punctatus Agassiz. Bottom net in 18 metres, Osu trawl, 2. (New record.)
Ostracion (*Acanthostracion*) *tricornis* L. Chorkor seine, Osu trawl and mouth of Densu, 9. (Irvine, p. 215.)
Hemiconiatus guttifer (Bennett). Accra, 1. (Irvine, p. 217, as *Ephippion*.)
Tetrodon pustulatus Murray. Chorkor seine, 50. (Irvine, p. 217.)
Lagocephalus laevigatus (L.). Chorkor seine, 4. (Irvine, p. 216.)
Spheroides spengleri (Bloch). Axim, 1. (New record.)
Diodon maculatus Lacépède. Osu trawl, 2. (New record.)
Chilomycterus antennatus Cuvier. Chorkor seine and near Teshi, 3. (New record.)
Haplochilichthys loati (Boulenger). Mangrove swamp pool near Ada, pool near Tefle, Densu estuary, 13. (New record.)
Epiplatys sexfasciatus. Steindachner. Pokoasi dam, 1. (Irvine, p. 263.)

THE CILIATION AND FUNCTION OF THE LABIAL PALPS OF *ACILA CASTRENSIS* (PROTOBRANCHIA, NUCULIDAE), WITH AN EVALUATION OF THE ROLE OF THE PROTOBRANCH ORGANS OF FEEDING IN THE EVOLUTION OF THE BIVALVIA

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(With 11 figures in the text)

The ciliation and structure of the labial palps of the nuculid *Acila castrensis* have been investigated and found to be extremely complex. A morphological and functional association of the labial palps and the inner demibranchs of the ctenidia has been observed in *Acila* and in *Nucula*. Small particles trapped by the ctenidia are passed to the labial palps and then to the mouth via the lateral oral groove. Nuculids have three ways of obtaining particles to be sorted for food : (*a*) by way of the ciliated palp proboscides ; (*b*) by way of the outer, unridged surfaces of the outer palp lamellae the ciliation of which collects particles from the incurrent stream of water ; and (*c*) by way of the frontal and enlarged frontal cilia of the ctenidia and the functional association of the ctenidia and palps. Comparisons are made from which it is shown that the Nuculidae and the Tellinacea share certain adaptations for *inhalant* deposit feeding in muddy environments. Morphological, paleontological, and embryological evidence is reviewed. The conclusion is reached that the immediate bivalved ancestors of existing protobranchs, filibranchs, and eulamellibranchs could have been suspension feeders and that palp proboscides may never have appeared in the evolutionary mainstream of the Bivalvia.

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INTRODUCTION

Prior to the work reported here, the ciliary patterns on the labial palps of the Nuculidae have not been thoroughly studied. The present paper, a segment of a larger work on the structure, function, and evolution of the labial palps of bivalves, is offered separately because the ciliary pathways of observed nuculid palps comprise a pattern unique within the class.

Nuculids possess one labial palp on either side of the body. Each is divided into a palp proboscis, a palp pouch, and two palp lamellae. The terms are those of Hirasaka (1927), who first gave distinctive names to the regions of the palp, although Mitsukuri (1881) originally described them.

All authors (cf. Yonge, 1939, p. 114) agree on the basis of observation that the palp proboscis of each palp is a tentacle-like feeding organ having the capacity to reach out between the shell valves and to gather particles from the substratum. These particles are led by ciliary activity on the proboscis to the inner face of the palp pouch from which they are transferred to the ridged apposed surfaces of the palp lamellae. Here the particles are sorted on the ridges, apparently according to size alone, with some particles eventually reaching the mouth as food. The general arrangement of these organs within the mantle cavity is shown in Fig. 1.

However universal the foregoing agreement may be, there are differences of opinion regarding the palp-ctenidium relationships, the facts of which are significant for our understanding of bivalve evolution, since the Nuculidae are regarded as the most primitive living members of the class (Yonge, 1939).

The present paper is concerned with the general anatomy and details of ciliation of the labial palps of the nuculid, *Acila castrensis*, and with the association of the palps and ctenidia in this species. The general morphology, the major ciliary tracts, and the palp-ctenidium relationships of *Nucula tenuis* Montagu have been found to be the same as those of *Acila*. The findings reported and the conclusions drawn in this paper are believed to apply to both species. The Discussion deals with the influence of new facts upon an understanding of the place of the Nuculidae in the evolution of the bivalves.

METHODS AND MATERIALS

Acila castrensis is common on muddy bottoms of the straits and channels of the San Juan Archipelago which lies near the mouth of Puget Sound, Washington, but most of the material used here came from Bellingham Bay off the nearby mainland. More than one hundred individuals were used in the following observations. Specimens to be anaesthetized were placed in a 1 : 1 mixture of seawater and isotonic magnesium chloride for two or three days, or until they no longer responded to prodding. In all instances, the specimen under observation was disposed of at the first sign of deterioration. Both excised and intact palps were observed, the former being pinned out with fine insect pins under water. The relationships of palp and ctenidium were

seen by shining a bright light between the shell valves, these being forcibly separated about 1·5 to 2 mm. Details of ciliation were determined by placing in any particular area a few particles of " Aquadag ", a commercial graphite lubricant manufactured by the Acheson Colloids Company, Port Huron, Michigan. A fine insect pin (size 00) was used to transport a small amount of Aquadag to the area of observation from a mass of this substance placed nearby in the dissecting pan. In subsequent studies, after acquaintance with the ciliary tracts was established, the amassed material found between the palp lamellae of freshly-opened specimens was often used undisturbed for tracing functional relationships between tracts or areas of the palps.

Section 1. FORM AND CILIATION OF THE LABIAL PALPS

Observations

The structure of the palp will be dealt with in the sequence by which particles pass when collected by the palp proboscis.

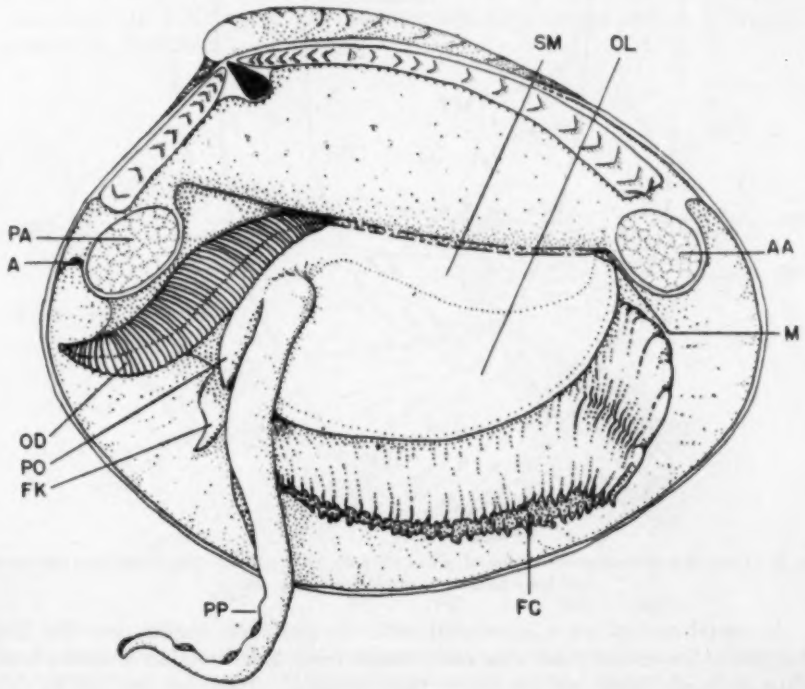


Fig. 1—*Acila castrensis*. Organs of the mantle cavity as seen from the right side. (Key to lettering, p. 538.)

The palp proboscis. There is one palp proboscis on the outer lamella of each of the two labial palps (Fig. 1). Each proboscis is a very long, extensible

feeding organ having along the length of its posterior surface a trough, the ciliated epithelium of which has secretory (mucous) cells scattered throughout as reported for *Nucula* (Hirasaka, 1927). There are two types of ciliary tracts in the trough (Fig. 2). A major tract originating near the crest of each wall of the trough consists of cilia which beat obliquely towards the floor of the trough. This tract gradually becomes parallel to the long axis of the proboscis until particles on the floor itself are led proximally between the shell valves and into the region of the palp pouch.

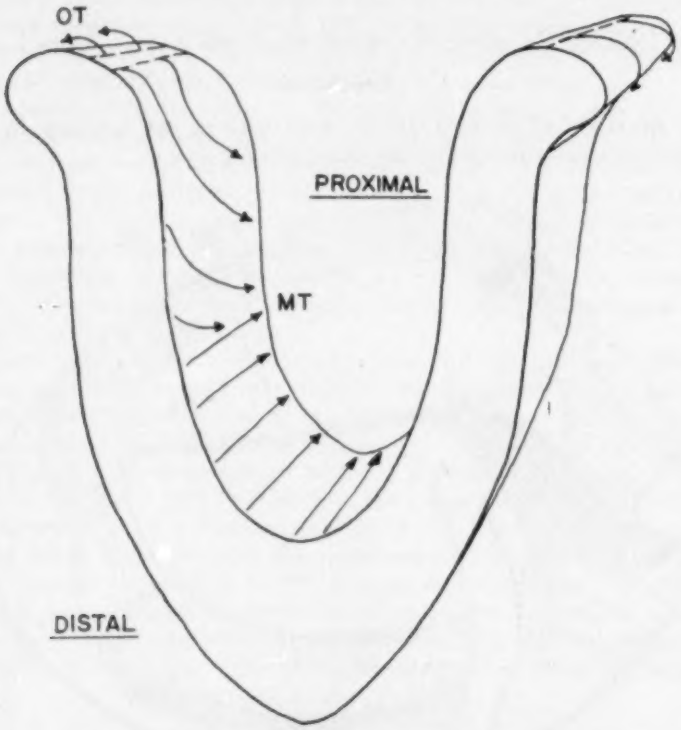


Fig. 2—Three-dimensional cross section of one of the palp proboscides. Arrows indicate direction of ciliary beat. (Key to lettering, p. 538.)

A second sort of tract associated with the proboscis begins near the line of origin of the major tract near each trough crest, the direction of ciliary beat being *outwards* from the trough in this instance. Particles are led in this second kind of tract to points immediately over the crest of the trough on each side where they remain wrapped in mucus. Such bound particles are discarded when the proboscis is retracted into the mantle cavity. The outwardly beating cilia of the second tract continue around the distal end of the proboscis. The outer surface of the proboscis is unciliated.

At its proximal end, the proboscis fuses with the outer surface of the outer palp lamella and palp pouch, its musculature passing into the body to fuse with the posterior retractor of the foot as was reported in *Nucula* by Hirasaka (1927).

The proboscides are sensitive to the least jarring of the dissecting pan or to the slightest touch of a probe—withdrawing quickly between the shell valves, which close after them. Within the mantle cavity, the proboscides curl in the direction of their anterior, unciliated surfaces and lie against the outer palp lamellae in planispirals, the ciliated troughs facing away from the centres of the spirals.

The palp pouch. Particles passing proximally in the trough of the palp proboscis are transferred within the mantle cavity to the palp pouch, a flap-like structure with a concave inner surface and a convex outer surface. In the normal position, the morphologically ventral and anterior margins of the pouch lie inserted between the walls of the proboscis trough (Fig. 3). The morphologically posterior margin lies inserted between the posterior margins of the palp lamellae. The margins inserted between the walls of the proboscis trough may be withdrawn, but the functional significance of such a change in position is unknown.

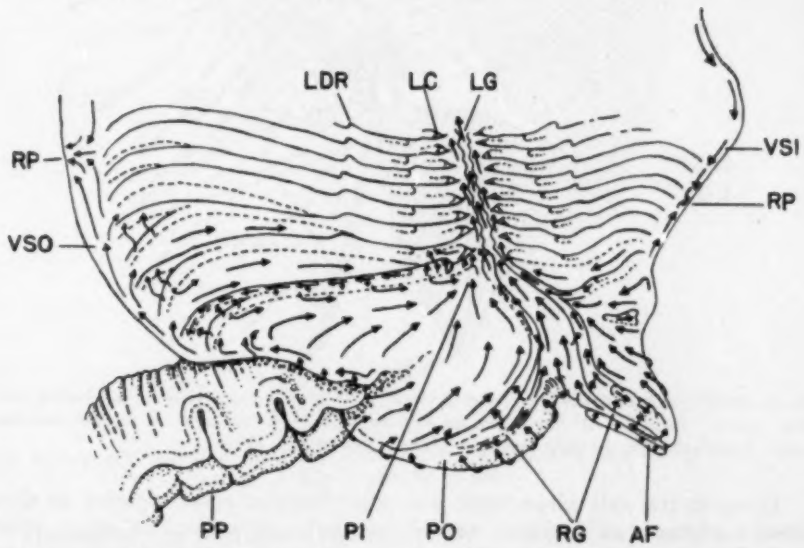


Fig. 3—Morphological and ciliary relationships at the posterior end of the right labial palp. The apposed faces of the palp lamellae have been widely parted. (Key to lettering, p. 538)

Particles in the proboscis trough are picked up by ciliary tracts on the inner surface of the palp pouch and are led along its broad concave surface to the most posterior regions of the palp lamellae. Other ciliary tracts exist on the palp pouch, but as they are not concerned with feeding via the palp proboscis, they will be discussed later.

The palp lamellae. Each of the two labial palps has an inner and an outer lamella which hang down side by side from a common dorsal suspensory membrane that is itself fused to the dorsal wall of the mantle cavity for the entire length of the lamellae (Fig. 1). The length of each lamella is approximately one-half that of the shell. The apposed faces of the lamellae bear a series of parallel ridges, hereafter called folds of the lamellae, lying perpendicular to the palp axis. The groove between any two folds is here termed a sulcus. In individuals measuring 16 mm. in shell length, there are about 67 folds per lamella; fewer in smaller animals. The folds near the mouth (Fig. 4), which lies surrounded by the anterior ends of the lamellae, are very narrow, but succeeding folds become progressively larger towards the posterior margins of the lamellae where particles to be sorted for food are received.

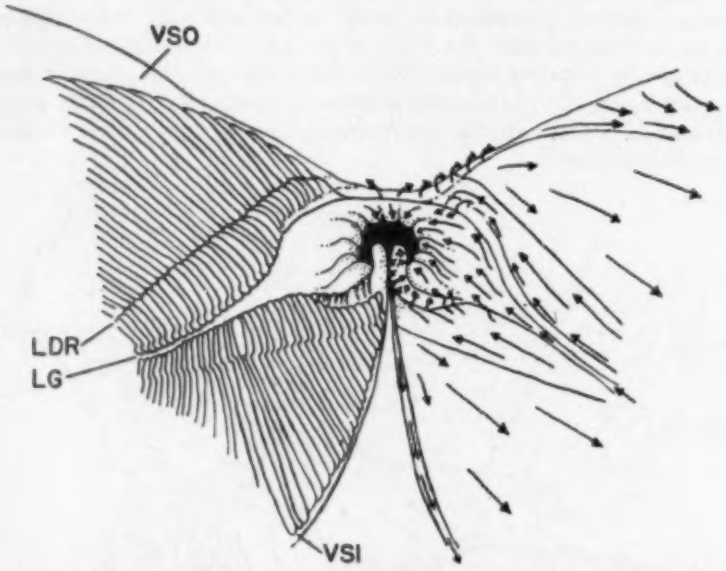


Fig. 4—Relationship of the palp lamellae to the mouth. The apposed faces of the lamellae have been parted. Direction of ciliary beat on exposed surfaces is indicated on the left lamellae. Folds are indicated on the right lamellae. (Key to lettering, p. 538.)

Lying in the axis where inner and outer lamellae come together at their dorsal margins is an unridged, narrow " lateral oral groove " (Kellogg, 1915) in which cilia carry particles from the posterior ends of the lamellae to the mouth.

The ventral margins of the apposed faces of the lamellae are unridged, this region being much wider on the outer lamella. In the natural state, when the lamellae are directly apposed, the ventral margin of the outer lamella is folded over that of the inner lamella except in the most posterior portions. Cilia along the ventral margins of both lamellae beat posterad on the anterior and central parts, while on the postero-ventral margins, the cilia beat in an anterior

direction. These opposed currents meet in a restricted area where the cilia beat towards the ventral margin (Fig. 3, RP). Pseudofeces are formed here and are passed to the heel of the foot, which bears ciliary rejection currents.

The broad *unridged* outer surface of the outer lamella (Fig. 5) bears cilia which beat towards the ventral margin. Immediately anterior to the point of fusion of the palp proboscis with the outer lamella, the general ciliation is altered and particles placed there are led dorsally and then either posteriorly around the base of the proboscis or anteriorly and then ventrally in a curved path.

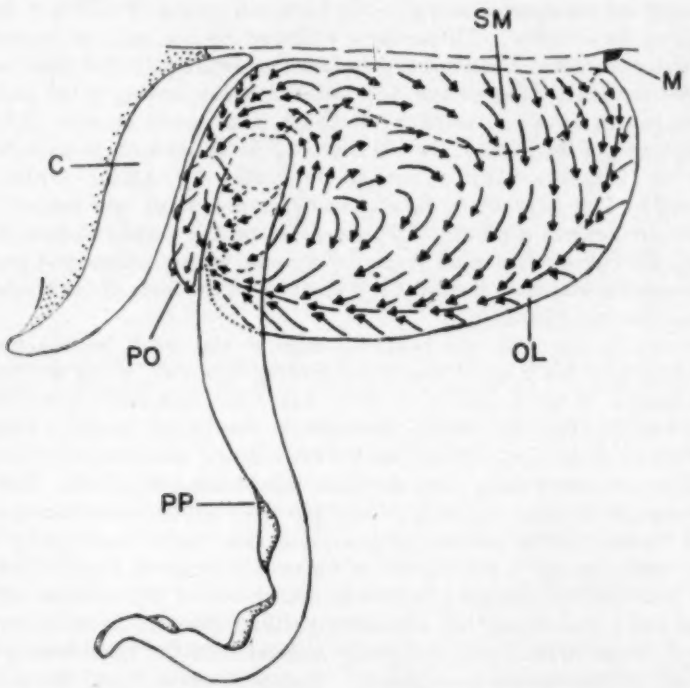


Fig. 5—Unridged surface of the right outer palp lamella showing direction of ciliary beat. (Key to lettering, p. 538.)

Cilia along the ventralmost margin of the unridged surface of the outer lamella beat postero-dorsally. Where this and the general ventrad tracts meet a short distance from the ventral margin, a third tract of cilia is found beating posteriorly, parallel to the ventral margin of the outer lamella.

All particles placed on the outer surface of the outer lamella are led to the area of the palp pouch. Particles may be transferred across the outer face of the pouch and over its posterior margin to the inner surface (Fig. 3), or over the postero-ventral margin of the outer lamella, depending upon the initial direction taken by the particles around the base of the proboscis.

The unridged face of the inner lamella lies against the foot and is largely unciliated except for a narrow band along the free margin. Cilia of this band carry particles posteriorly to the point where the rejectory tracts on the *inside* of the ventral shelf converge. Here the particles are carried over the edge of the ventral margin and form a portion of the pseudofeces. Normally, the anterior and central margins of the inner lamella are covered by the overfolded ventral margin of the outer palp lamella. Thus the posterad currents on these two areas form a functional rejectory entity. Posterior to the point of convergence of these rejectory tracts, particles on the margins of the unridged surface of the inner lamella are carried directly over the edge of the margin and are transported along to the folds and sulci as a source of food.

Folds of the lamellae. All particles collected by the palp proboscides or by the outer surfaces of the outer palp lamellae eventually find their way to the ridged (apposed) faces of the palp lamellae where sorting of the particles, now wrapped in mucus secreted by the gathering organs, occurs. Although the complexity of the folds of the lamellae of *Nucula* has been, in part, demonstrated by Hirasaka (1927), further elaborated by Atkins (1936), and mentioned by Yonge (1939), no detailed study has previously been made of them.

There are several distinctly different areas on the ridged surface of each lamella. Except for the most posterior regions, where masses and particles first contact the lamellae, the form and ciliation of the folds of both inner and outer lamellae are identical.

Particles coming over the posterior edge of the outer lamella from its unridged surface are trapped in a tract leading anteriorly along the posteroventral margin of the lamella to a point where the first fold approaches the ventral margin (Fig. 3). Here the particles are swept dorsally along the posterior wall of the first fold and are led towards the lateral oral groove along with those particles coming from the inner face of the palp pouch. The point of convergence of these tracts is a large pit (Fig. 3, PI) formed mainly by a ventrad folding of the median palp axis in this region, and partly by an enlarged palp " crypt ", the details of which will be given later. This pit is further enlarged by the atrophy of the dorsal end of the crest of the first lamellar fold. Just below the atrophied portion, this fold becomes suddenly high and, in the normal position, makes contact with the ridge bounding the outer side of the lateral oral groove. Masses received from the proboscis together with particles passed from the outer surface of the outer lamella may be seen to be " packed " into the pit region and along the length of the first fold where they form a very large compact mass. Smaller masses and particles torn by ciliary activity from the larger accumulation are passed over the crest of this fold. With this step, sorting of the gathered particles begins.

The sorting areas of the lamellar folds are complicated by the presence of several ciliary tracts on each fold. As an aid in describing the complex process of sorting, each distinctive ciliary tract has been given an arbitrary number. Direction of ciliary beat is not always given in the following description ; reference to Figs. 6 to 9 is thus essential. The number of different ciliary tracts on any fold varies according to the position of the fold on the lamella : the posterior folds possess fewer tracts than do more anterior folds. In general,

there are three *classes* of ciliary tracts on the lamellar folds : " acception tracts " move particles *towards* the mouth, " rejection tracts " move particles *away from* the mouth, and " accessory tracts " move particles into or out of acception or rejection tracts.

Of the masses moved across the most posterior fold from the accumulated mass in the " pit ", those with diameters exceeding the height of the posterior folds are passed anteriorly on the crests of the posterior folds in two ciliary tracts labelled " 2 " and " oral-9 " (Fig. 6). Tract 2 is greatly expanded on

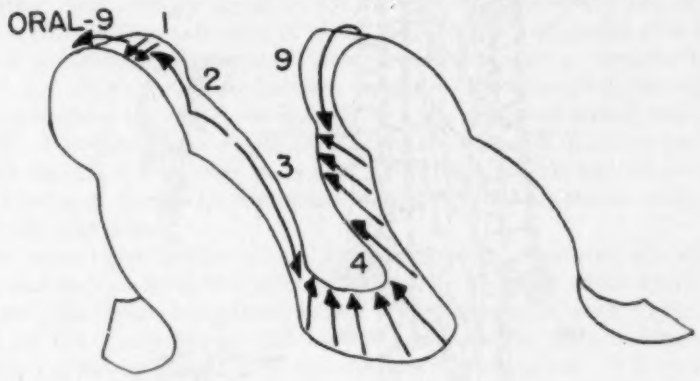


Fig. 6—Two folds from the posterior region of a palp lamella as they would appear in three-dimensional cross section when viewed from their more ventral ends. Anterior is to the left.

the ventral part of the three most posterior folds and is sunken into a shallow groove in that region. Larger masses are retained on the crests because of their size. As they are passed from crest to crest, such masses are caught by tract 1, a narrow ventrad tract separating tracts 2 and oral-9, and are led gradually to the ventral margins of the palp lamellae where they are passed as pseudofeces to the point of rejection. Smaller masses and particles torn from the larger masses to be rejected may be moved from these rejection tracts into the grooves (=sulci) between folds to acception tract 4. This transfer occurs under the influence of tract 3 and part of tract oral-9. These tracts, 3 and oral-9, also function as " retainer " tracts, keeping particles in tract 4 in place.

Anterior to the first fold, the complexity of structure and of ciliation of the folds and sulci increases. (Reference to Fig. 7, A–E will be helpful in understanding spatial relationships.) The folds, although increasing in complexity, become narrower, their crests grading from 0·2 mm. across in the posteriormost fold to 0·04 mm. across in folds about the mouth. These measurements were taken from an animal 14·5 mm. in total shell length with the outer palp lamella possessing about sixty-five folds and measuring 7·4 mm. in length.

Tract 4, which carries particles dorsad, divides about one-third the way from the ventral end of the sulci. Between the divisions of tract 4, a new tract appears on the floor of the sulcus. Because of the very long cilia which beat obliquely and lead particles bound in mucus dorsad with a rotary motion,

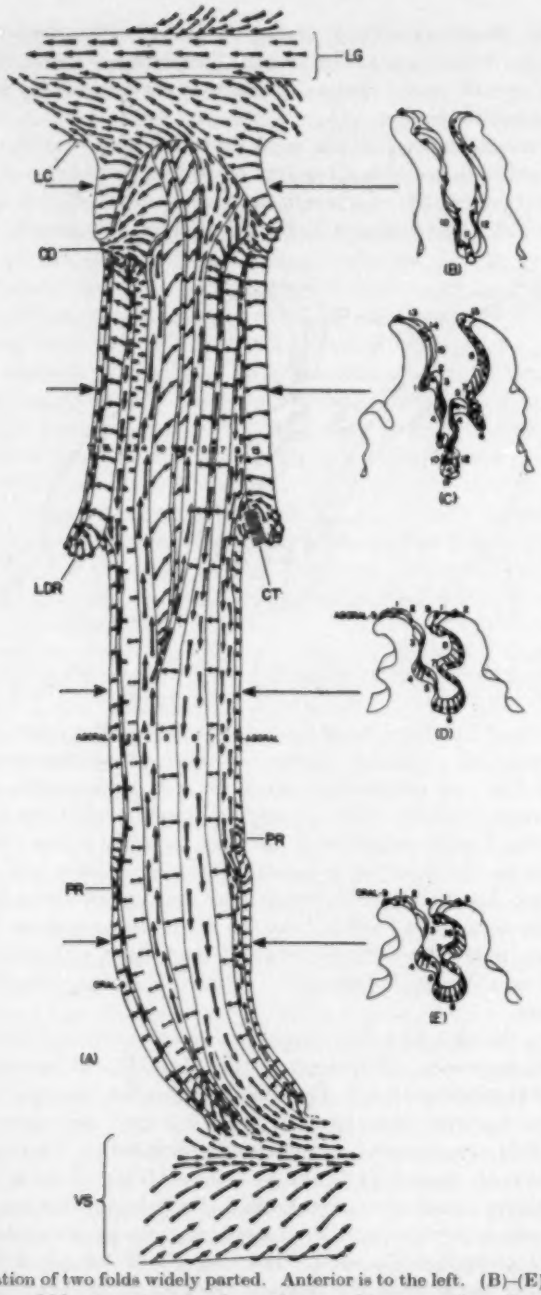


Fig. 7—(A). Ciliation of two folds widely parted. Anterior is to the left. (B)–(E). Contours and ciliation of the two folds at various levels as they would appear three-dimensionally. The relationships are somewhat distorted for diagrammatic purposes. (Key to lettering, p. 538.)

the new tract may be recognized as distinct from tract 4. There appear to be three subtracts comprising this new tract, the designation of the entire tract being " 10-11-12 ". The cilia of 11 are somewhat longer than those of 10 or 12. Where tract 10-11-12 begins in the sulcus, the great majority of the smallest particles are moved from tract 4 into tract 10-11-12 and are very firmly wrapped together in a mucous rope. This rope is rotated about its long axis and is moved dorsad towards the lateral oral groove. If the sulcus is oriented as that diagrammed in Fig. 7, A, the rotation of the mucous rope is counter-clockwise. Immediately distal to the lateral oral groove the mucous rope enters a blind-ending extension of the sulcus beneath and roofed over by the tissue of the lateral oral groove. This extension is termed a " lamellar crypt " (Fig. 7, A). One crypt exists between every two folds except in the region of the mouth where the sulci open directly into the expanded lateral oral groove (Fig. 4). Posteriorly, the crypts become larger and larger until the last crypt on each lamella is relatively huge and widely open. This last crypt on the outer lamella is greatly hypertrophied and forms, in conjunction with a palp sulcus, the palp pouch.

The entire inner surface of each crypt is ciliated. Tracts on the aborally facing wall lead particles to a point just dorsal to the point where a new tract, 1, begins ; this region being termed the " crypt depositional zone " (Fig. 7, A). Tracts on the orally facing wall lead particles to the margin forming the " ceiling " of the crypt, and then into the lateral oral groove. It is clear that the mucous rope in tract 10-11-12 is rotated against the dorsal wall of the crypt. Particles and small masses may be released from the rope and led onto one or other wall of the crypt as described above. More commonly it has been observed that the entire mucous rope is transferred slowly out of tract 10-11-12 to the crests of the folds adjacent to the lateral oral groove. These masses are gathered together from the serially arranged crypts and pass anteriorly to the mouth.

Particles remaining in tract 4 after the appearance of tract 10-11-12 are wrapped loosely in mucus and are either squeezed out at the crypt depositional zone and transported from crest to crest anteriorly or pushed up into tracts 1 and 8 and carried ventrally. The latter occurs when there is more material coming in from tract 4 than can be readily carried away on the crests.

The foregoing description applies to all folds and sulci. However, other tracts appear, and the disposition of some of those already mentioned changes on more anterior folds.

In the third sulcus from the posterior end of the lamella, tract 10-11-12 is depressed into a deep and separate groove in the floor of the sulcus (Fig. 7, C), thereby elevating the divisions of tract 4 to the walls of the folds. A new ventrad tract, 6, represented as a very short tract just posterior to tract 10-11-12 in the posterior four or five sulci, makes its way to the ventral end of the sixth sulcus. Dorsally, on the oral face of each fold, tract 6 lies in a separate groove, the lips of which are in tight contact with one another. Ventrally, where tract 10-11-12 finds its origin about one-third the distance from the ventral edge of the lamella, tract 6 becomes located on the floor of the sulcus (Fig. 7, D). The first complete tract 6 empties onto the ventral

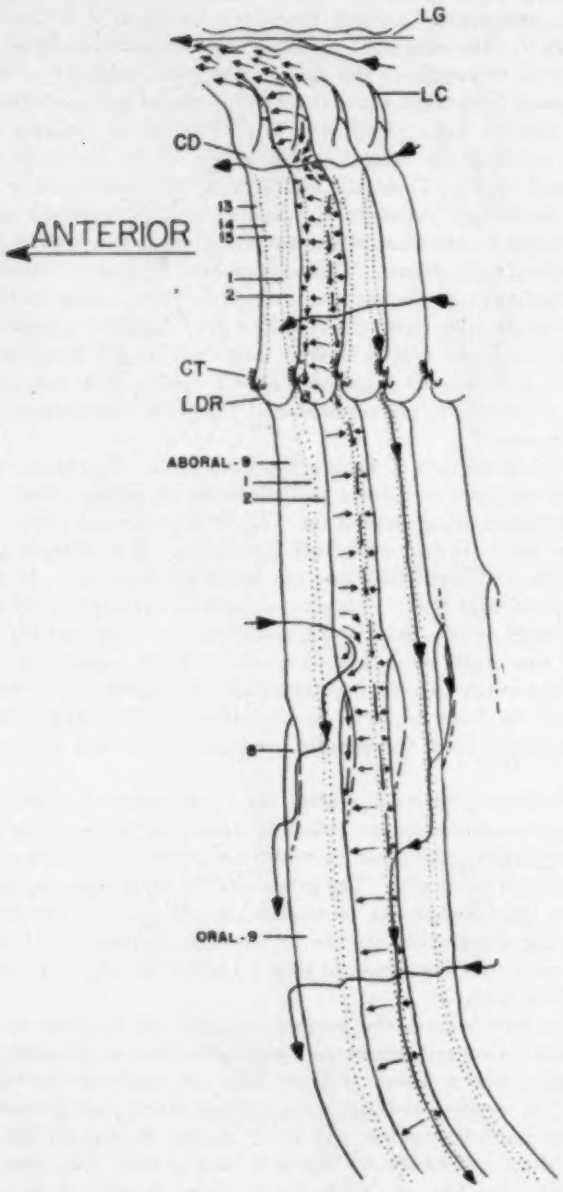


Fig. 8—Portions of five folds showing normally exposed tracts (small numbers), direction of ciliary beat of the tracts (small arrows), and common pathways taken by particles (large arrows). (Key to lettering, p. 538.)

shelf of the palp lamella at the point where pseudofeces are formed (Fig. 3).

A further complication is the appearance of a high crest on the dorsal quarter of each fold (Fig. 7, C). Such crests terminate abruptly at their ventral ends in blunt projections, each of which bears a tuft of long cilia on the oral surface. These ciliary tufts create a barrier between the dorsal and ventral sections of the folds in two ways. Firstly, a segment of each tuft reaches across from the oral surface of one projection to the aboral surface of the next anterior projection. This does not involve an actual ciliary junction ; the cilia simply touch the aboral surface. Secondly, a segment of each tuft seems to reach across to meet a similar tuft on the opposite lamella and to form a ciliary junction thereby. The wall created by the juxtaposition of the blunt projections is here called the " lamellar division ridge " (Figs. 4, 8, LDR). The heightened crest on the dorsal segment of each fold bears three ciliary tracts not represented on the fold ventral to the lamellar division ridge. These tracts are numbered 13, 14, and 15. Large masses and mucous ropes, two or more folds wide (and received from tracts 4 or 10-11-12), are moved steadily forward by tracts 13 and 15 (Fig. 8). Tract 14, seeming at first sight to be an incongruous ventrad (rejection) tract in a position of general acceptance, is weak, but large masses above the lamellar division ridge have been seen to be moved ventrad by it. It appears that tract 14 deflects such masses and ropes passing towards the mouth away from other mucous ropes emerging from tracts 4 and 10-11-12 near the lateral oral groove. Tract 14 is not powerful enough to drive masses past the ciliary junctions between lamellae at the lamellar division ridge.

Individual particles of large size and small mucous masses torn from larger masses tend to be trapped by tracts 1 and 8 above the lamellar division ridge. Such particles and masses are led into the region below the lamellar division ridge where they come under the influence of other ciliary tracts.

On the seventh fold from the posterior edge of the lamella, that is, one fold anterior to the sulcus first bearing a " complete " tract 6, a posterad tract 9 (=aboral-9) appears. Aboral-9 occupies a very short length of the seventh fold just under the lamellar division ridge, while the remainder of the fold possesses a tract 9 beating anterad (=oral-9). From this seventh fold forward, the proportion of the crest given to tract aboral-9 becomes greater with each fold (Figs. 7, A and 8) until in the general region of the twenty-second fold (counted from the posterior end of the lamella) tract oral-9 disappears and all crests of the twenty-five or thirty anterior folds are occupied by tract aboral-9 only. That is, ventral to the lamellar division ridge, particles on the crests of the folds are carried *away* from the mouth on the anterior half of the lamella but *towards* the mouth on the posterior crests. The two opposing ciliary pathways formed by tracts oral-9 and aboral-9 meet along a diagonal line formed by the turning points of tracts 9 (Fig. 9).

The mouth (Fig. 4) is surrounded entirely by acception tracts, namely, the expanded lateral oral groove (the " proximal oral groove " of Kellogg, 1915, p. 629) and the area of the lamellae dorsal to the lamellar division ridge.

As particles in tract 1 emerge below the lamellar division ridge, they are held in that tract by tracts aboral-9 and 2 until the place of reversal of tract 9 (Fig. 8). The particles may then be subjected to further sorting as they are shifted from fold to fold by tracts 2 and oral-9. Particles and masses shifted from crest to crest in tract oral-9 eventually meet the turning point of tract 9 unless they are small enough to be carried into a sulcus before the turning point is reached. If a mass *is* carried to the turning point, it may be shifted back and forth between tracts oral-9 and aboral-9 (Fig. 8). By the ventrad action of tract 1 and the small section of tract 8 exposed in the vicinity of the turning point of tract 9 on each fold, the mass is led to the ventral shelf of the lamella from which it is expelled as part of the pseudofeces.

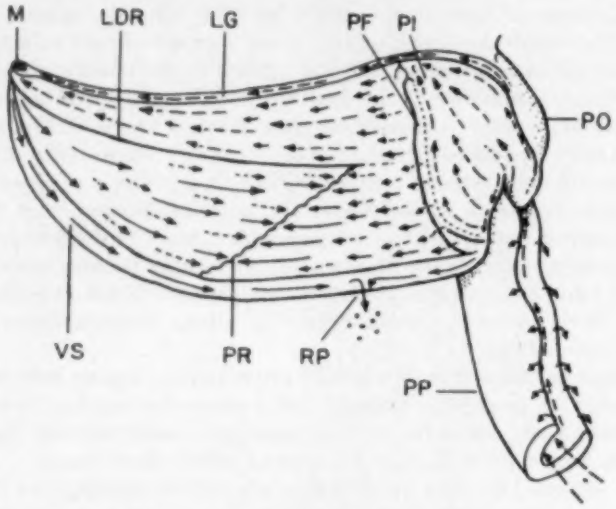


Fig. 9—Scheme of the general ciliation on the ridged surfaces of the right outer palp lamella. Relative probability of acceptance of particles (dashed arrows), or of rejection of them (entire arrows), is proportional to the length of the arrows drawn on each region of the lamella. (Key to lettering, p. 538.)

Particles moved ventrally in tract 8 from the region above the lamellar division ridge are likewise subject to further sorting, generally being shifted to tract 4 below the lamellar division ridge. If particles are driven in tract 8 to the place where this tract is exposed immediately below the turning point of tract 9, they are likely to be rejected unless small enough to fit into the sulcus ventral to that point. Just ventral to the exposed segment of tract 8, this tract ends, and in its place a dorsad tract, 16, also has its termination after traversing the more ventral segment of the oral face of the fold (Fig. 7, A and E). The function of tract 16 is not fully understood. However, by its position and direction of ciliary beat, it is most probably supplementary to tract 4, particles in tract 16 being shifted to tract 4 at the termination point of tract 16.

Particles passed, in some unknown fashion, into tract 6, which is tightly closed above and below the lamellar division ridge, are not re-sorted, although small particles are removed from tract 6 through the activity of tract 5.

Particles and masses easily transported in individual ciliary tracts on the larger posterior folds are handled as if they become proportionately larger as they are passed forward to smaller folds and sulci bearing comparable but narrower tracts. Therefore, particles led ventrad from above the lamellar division ridge in tracts 1 and 8 are likely to be carried in tracts 9, either anterad or posterad, to the turning point of tract 9 and rejected unless, apparently through chance, a tract 3 large enough to accommodate the particles is encountered. The particles are then re-sorted, either to undergo similar treatment again, or to be led to acceptory paths towards the mouth by tract 4.

Tracts such as 3 and 7 function as " retainer " tracts. That is, by their action they retain particles or masses in an adjacent tract, thus preventing haphazard shifting about of particles or masses in the major acception and rejection tracts. Tract 2 functions as a retainer tract above the turning point of tract 9 (Fig. 7, A), but becomes a major anterad tract below that point. Tract 5 seems to combine the retainer function with that of removing small particles from tract 5 into acception tract 4. At the dorsal and ventral ends of the folds and sulci, retainer tracts become rejection or acception tracts depending upon the direction of ciliary beat of the major tract towards which they beat (Fig. 7, A).

Contours of the lamellar folds. Particles and masses moving in the ciliary tracts of the folds are somewhat isolated, one from the other, by rather complex bends, thickenings, and grooves on the folds (Figs. 6, 7, B–E). The crests of the posterior-most folds (Fig. 6) lie in a narrow indentation on the aboral face of the next fold anterior. This arrangement separates particles moving in a tract 4 from the masses transferred across the crests of the folds.

Above the lamellar division ridge, tracts 7 and 5 are pressed together, thus isolating tract 6 from other tracts (Fig. 7, C). Tracts 7 and 5, as a unit, are in juxtaposition to tracts 3 and 4 on the opposite wall of the sulcus.

Expansions of tract 10-11-12 (Fig. 7, B and C) are in contact in the living animal. This contact effectively creates a tube through which the mucous rope in tract 10-11-12 is sent dorsally while being isolated from more crest-ward regions.

The crest of one fold above the lamellar division ridge is capable of bending across to the next fold anterior and may lie in the groove of tract 1 or any place on tract 15 (Fig. 7, C).

Below the lamellar division ridge, the projecting shelf upon which tract 7 is found over-lies the shelf bearing tracts 4 and 5 of the next fold anterior (Fig. 7, D). This configuration results in the isolation of tract 6. The crest of the fold bends anterad, contacting the shallow groove on the fold next anterior.

All the spatial relationships described above appear to represent the more usual situations, but all such contours may be altered by muscular contractions that may involve all of both palp lamellae, two or more entire folds, or a localized region of a single fold. For example, in one freshly-opened *Acila*,

there was a very large mass of particles in mucus between the posterior ends of the palp lamellae below the lamellar division ridge. The entire palp underwent contractions that had the effect of scraping one lamellar surface against the other. As the contractions occurred mainly in the region about the mucous mass, the palp lamellae acted as a sort of bellows, pushing small particles torn from the mass anteriorly and out into the mantle cavity through the artificially parted palp margins. Possibly, in the intact organism, this bellows-like action has some transport function.

The inner and outer palp lamellae may press so closely together that their folds interdigitate. Large masses of particles bound in mucus have been seen to be moved between such apposed lamellae, the lamellae parting locally around the masses. By the pressure upon the mass, small particles are frequently torn away and led into tract 4.

By the spreading apart of any two or more folds, the depths of the sulci are exposed, allowing many particles to enter the deeper tracts and to bypass the usual routes.

Individual tracts may "ripple" dorso-ventrally allowing a very local modification that will, as in the common case of tracts 2 and 3, expose or cover tract 3. If tract 3 is exposed, particles are led deeper into the sulcus. If tract 3 is covered by the next fold posterior, particles miss the sulcus entirely. These very localized alterations are extremely important in the passage of small particles into acception tracts within the sulci.

CONCLUSIONS OF SECTION 1

1. The palp proboscides are definitely feeding structures, as reported by other investigators. Although not proved, it is probable that some selection of particles by size occurs on the palp proboscides. This is indicated by the presence of rejection tracts on the crests of the walls of the trough. Drew (1901, pp. 334 and 354) has shown that the palp proboscis and the palp pouch are each embryologically derived from the outer palp lamella and that each consists of two folds with a sulcus. The ciliation of the palp pouch is certainly derivable from that of a sulcus and a lamellar crypt of the sort found just anterior to the palp pouch. However, the ciliation of the palp proboscis is somewhat problematical. The tract on the floor of the trough may represent tract 4, the oblique trough-ward tracts on either side may represent tracts 3 and oral-9, and the outwardly beating tract on the inner crest may represent tract 2. But the outwardly beating tract on the outer crest of the proboscis has no counterpart on the usual folds.

2. Particles that contact the outer surfaces of the outer palp lamellae are gathered as a source of food. These particles and the material collected by the proboscides are led to the posterior ends of the palp lamellae where the large individual tracts and the hypertrophied sulci containing only dorsad tracts indicate, and observation substantiates, that all particles large and small, and wrapped in mucus, are massed together indiscriminately. Only later are the components of the mass segregated, probably by size alone, through ciliary and muscular activity on a series of complex folds of the lamellae.

3. The interlamellar ciliary junctions at the lamellar division ridge divide the lamellae into dorsal and ventral areas. The ciliation upon the exposed areas dorsal to the lamellar division ridge is entirely concerned with acception except where locally modified through muscular action. Below this ridge, the ciliation of exposed surfaces causes rejection except in the posterior regions and in localized areas of modification by muscular activity (Fig. 9).

4. Rejection and acception tracts on the folds of the lamellae are isolated from one another by complex foldings or thickenings of areas adjacent to those tracts. Such foldings and thickenings bear accessory tracts of which some are " retainer " in function, keeping particles within acception or rejection tracts. Other accessory tracts combine the retainer function with that of actual transport of masses and particles.

Section 2. THE PALP-CTENIDIUM RELATIONSHIP OF *ACILA CASTRENSIS*

Observations

Functional morphology of the relationship. Each ctenidium of *Acila* (and of *Nucula* ss.) is composed of an inner and an outer demibranch, the components of which are thin ciliated platelets of leaflets placed side by side at right angles to the long axis of the ctenidium. Details of ciliation of the leaflets have been described and discussed by Orton (1912), Atkins (1936) and Yonge (1939).

Particles alighting on the frontal surface of the leaflets are passed from the outer tip of the outer (more lateral) demibranch across the entire edge of each pair of leaflets to the tip of the inner demibranch. Enlarged frontal cilia, which beat anterad, are found at the tips of the inner leaflets of the posterior third of the ctenidium. The anterior two-thirds of the inner demibranch does not possess enlarged frontal cilia of this sort.

In specimens relaxed in isotonic magnesium chloride, and in which the valves are parted 1·5 to 2 mm., just enough to permit observation of the mantle cavity, it can be seen that the entire margin of the inner demibranch anterior to the point where the line of enlarged frontal cilia terminates is in direct contact with the posterior margins of the palp (Fig. 10). From the point where the line of enlarged frontal cilia ends to the point where the two palp lamellae come together dorsally, the inner demibranch contacts two ciliary tracts, one along the posterior margin of the inner palp lamella, the other on the convex face of the palp pouch (Figs. 3 and 10, RG). These tracts are functional extensions of the lateral oral groove and, in the normal position, receive particles from the accumulation point where enlarged frontal cilia cease to exist on the inner demibranch and from the tips of leaflets just anterior to the accumulation point. As particles are shifted from the inner demibranch to the palp lamellae, larger particles bypass these narrow tracts, which lie in shallow grooves, and are passed either over the margin of the palp pouch to its concave surface or to the ridged surface of the inner palp lamella and are sorted in the manner described in Section 1.

Smaller particles shifted to the lamellae from the inner demibranch are led by the functional extensions of the lateral oral groove into the lateral oral groove proper lying in the axis between the palp lamellae and are passed to the mouth directly and *without sorting.*

Along the posterior margin of the palp, where it is fused to the body, is another small groove (Fig. 10, DG). The edge of the anterior half of the inner demibranch is set into this groove, and small particles are led by the cilia within the groove to join those particles received more ventrally from the inner demibranch. The ctenidium is not fused in any way to structures of the palp. Any contraction of the ctenidial axis may disturb the relationships, but these are re-established upon relaxation.

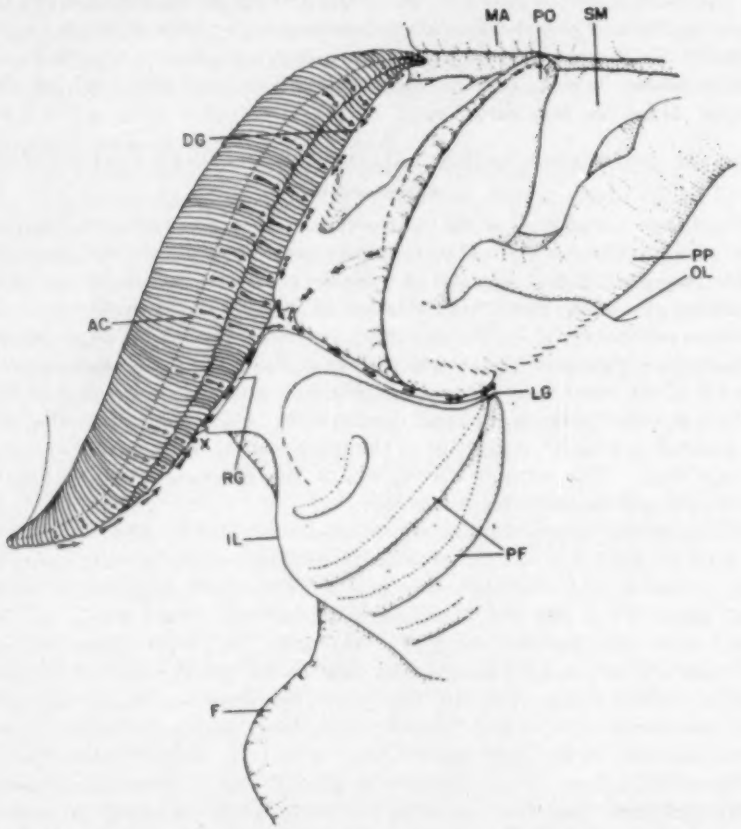


Fig. 10—The association of the right labial palp and ctenidium of *A. castrensis*. The palp pouch, proboscis, and outer lamella have been folded back. The reception groove indicated on the palp pouch normally lies adjacent to that on the inner lamella. (Key to lettering, p. 538.)

The accumulated mass at the anterior end of the line of enlarged frontal cilia is not always passed on to the palps as a source of food. In one observation, a rather large dissociated mass of Aquadag was allowed to settle down between the slightly parted valves of a specimen. Many of the particles fell upon the ctenidial platelets, the smallest of the particles being drawn between the platelets into the suprabranchial chamber. Larger particles were passed to

the inner edge of the inner demibranch in the typical manner, being wrapped in mucus on the way towards the accumulation point. The sharply keeled posterior portion of the foot (Fig. 1) moved slowly back between the ctenidia, separating them, and pushing the large Aquadag mass into the suprabranchial chamber. Through ciliary activity along the ventro-lateral margins of the keel of the foot, the mass was pulled back out of the suprabranchial chamber and led towards the tip of the keel. The foot, the cleft locomotory portion as well as the keel, was protruded through the parted valves, the cleft portion undergoing the usual expansive locomotory movements. When the foot was retracted back into the mantle cavity, the shell valves scraped the Aquadag mass from the keel. After completion of these movements, the ctenidia rejoined along the line of attachment cilia on the inner demibranchs to re-form the functional division of the mantle cavity into inhalant and exhalant chambers. There was also a contraction of the suspensory membranes, drawing the ctenidia sharply upwards. This motion probably aided the removal of particles from the suprabranchial chamber. The mantle surface within the suprabranchial chamber is lined by a hypobranchial gland that presumably functions by binding small particles in mucus prior to their elimination (cf. Yonge, 1939, p. 92).

On the exterior of the shell valves, from the umbones to the margin immediately anterior to a line corresponding to the internal division of the mantle cavity into infra- and supra-branchial chambers, a thickened band composed of particles cemented together and to the valves is often found. The region of extrusion of particles bound in mucus lies in the position of the ventral end of this band of cemented particles. Perhaps the agglomeration represents a small portion of the debris rejected, in the manner described above, during the entire life of the individual. The means by which the particles remain cemented together is unknown.

The ciliation of the mantle surface leads pseudofeces to the place where the keel of the foot is protruded. These pseudofeces are pushed out of the mantle cavity by the same motion observed to remove masses from the ctenidia. Also, the shell valves are capable of clapping motions that can forcibly drive particles from the mantle cavity.

Removal of particles from the incurrent water. The primary inhalant area in *Acila* is anterior, as it is in *Nucula* (Yonge, 1939, p. 92). Upon several occasions, when heavy jets of Aquadag were placed near the inhalant area of *Acila*, the force with which they were taken into the mantle cavity suggested the presence of a stronger current than could be created by the relatively weak lateral cilia of the ctenidia. The ciliation of the outer surfaces of the outer palp lamellae and of the mantle directs water and particles posteriorly, and it is probable that the cilia on these surfaces accounts for the strength of the inhalant current, which is much stronger than would be expected if created by the lateral cilia alone.

Aquadag taken into the mantle cavity through the anterior inhalant aperture was often found between the palp lamellae in the process of being sorted. To ascertain the role of the retracted palp proboscides in removing

particles from the incurrent water and in transmitting them to the palp lamellae, the following experiment was performed :

Twenty large *Acila* were kept in filtered sea water for ten days. At the end of this time five specimens were dissected, and it was found that the digestive tracts of all five were devoid of particulate matter. The proboscides of ten of the remaining fifteen animals were completely removed with iridectomy scissors. These individuals and the five specimens still in possession of proboscides were placed in a dish containing about three millimeters of loose, easily disturbed, sediment composed mainly of Aquadag. The sediment was not deep enough for *Acila* to burrow in, and the specimens lay on their sides with the ventral margins of the shell valves just above the surface of the sediment.

Two days later all fifteen specimens were dissected, and the particulate content of the mantle cavity and of the digestive tract determined in each. The relative amounts of particulate matter found between the palp lamellae, in the stomach, and in the intestine are summarized for both groups in Table 1 below.

Table 1—Relative amounts of particulate matter found in the mantle cavities and in the digestive tracts of specimens with and without palp proboscides. (−, none observed ; +, very little to a little ; ++, moderate quantity ; +++, much, the organ often being quite packed with Aquadag.)

	Controls					Experimentals									
	1	2	3	4	5c	1	2	3	4d	5	6	7	8	9	10
Between palp lamellae	−a	+++b	+	−	−	+	+	+	−	+	++	+	−	+	−
In the stomach	−	+++	−	−	+++	++	+++	+	++	+++	+++	+++	−	−	−
In the intestine	−	+++	+	−	+++	+++	+++	+++	++	++	+++	++	++	−	+

a. Large mucous mass of Aquadag on outside of right palp lamella and on right ctenidium.
b. Some Aquadag in proboscis trough of both sides.
c. Left outer palp lamella torn.
d. Right inner palp lamella torn.

Because of the small number of specimens used in this experiment and because of the unnatural orientation of the specimens within the substratum, only one statement may be made with certainty : under the conditions of the experiment, specimens both with *and without* proboscides were able to collect particles that had gained entrance into the mantle cavity and were able in most cases to ingest the particles.

Besides the primary anterior inhalant area, there is a secondary or minor incurrent area just anterior to the point of contact of the posterior tips of the

ctenidia with the mantle. The position of this incurrent area corresponds to the point of protrusion of the palp proboscides and is present even when those organs are retracted into the mantle cavity. All pseudofeces are extruded from the mantle cavity through the aperture of this minor inhalant region.

CONCLUSIONS OF SECTION 2

1. A functional association of the ctenidium and palp lamellae of *Acila castrensis* has been observed. Ciliary tracts on the posterior margins of the palp lamellae are adapted for transporting fine particles from the inner demibranchs of the ctenidia either to the sorting areas of the palp folds or to the lateral oral grooves in which no sorting occurs and in which particles pass directly to the mouth.

2. *Acila castrensis* can, under the conditions of the described experiment, remove particles from the incurrent water. Particles of varying sizes must enter the mantle cavity in nature, for the ciliary beat creates a strong *incurrent flow* of water. Upon entrance into the mantle cavity, some particles, probably the largest, are rejected by tracts of the mantle. Other particles are led to the apposed faces of the palp lamellae by tracts of the unridged surfaces of the outer palp lamellae and by enlarged frontal cilia on the inner demibranchs. The very smallest particles are passed between the ctenidial leaflets into the suprabranchial chamber where they are probably trapped in mucus secreted by the hypobranchial gland and thrown out of the mantle cavity in the excurrent flow of water.

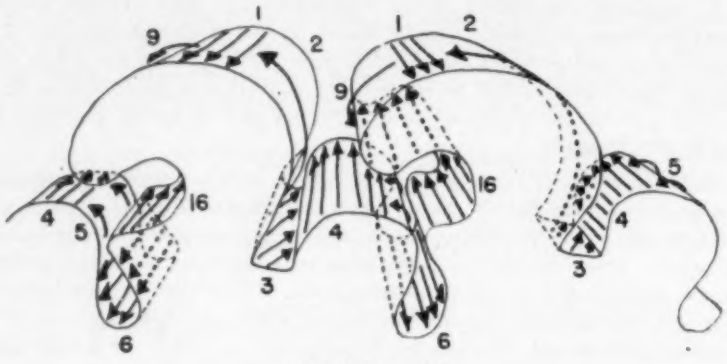
3. On the basis of evidence presented in this paper, it is concluded that *Acila castrensis* in nature removes particulate matter from the incurrent stream of water and sorts these particles as one of its sources of food. This species has, then, three ways of obtaining particles to be sorted for food : (*a*) by way of the extensible ciliated palp proboscides, (*b*) by way of the ciliation of the unridged surfaces of the outer palp lamellae, and (*c*) by way of the frontal and enlarged frontal cilia of the ctenidia and the functional association of the ctenidia and palps.

DISCUSSION OF SECTIONS 1 AND 2

Acila *as an inhalant deposit feeder*

Until disturbed, *Acila castrensis* remains buried just below the surface of the substratum (Schenck, 1936, p. 10). Yonge (1939, p. 82) has shown this to be the normal position of *Nucula nucleus* as well. Particles in the incurrent stream are, therefore, *received from deposits* as they are in many Tellinacea, which gather deposits from the substratum employing specialized incurrent siphons for that purpose (Yonge, 1949). Yonge has demonstrated that deposit feeding is universal in this group and that the relative sizes and complexity of the ctenidia and palps are associated with the *type* of substratum from which members of a species obtain their food. That is, where the substratum is firm of course, as in the environments of *Donax vittatus*, *Gari tellinella*, *G. fervensis*, *Solecurtus chamasolen*, and *S. scopula*, the ctenidia are relatively large, and the palps are relatively small. Where the substratum is muddy and

loose, as in the environments of *Macoma balthica*, *Abra alba*, and *Scrobicularia plana*, the ctenidia are relatively small and the palps relatively large, sometimes extremely so, as in *Macoma balthica*. The small size and the relative simplification of exposed surfaces of the ctenidia are achieved through reflexion and reduction of the outer demibranchs which, as in *Tellina* and *Macoma*, expose



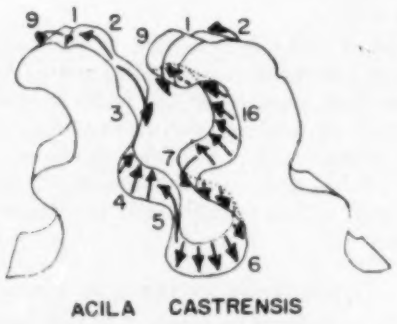


Fig. 11—Comparison of the contours and ciliation of two lamellar folds of *Macoma irus* with those of *Acila castrensis* as shown in Fig. 7, (E). Anterior is to the left.

the axis of each ctenidium to the incurrent water. Thus, as Yonge (1949, p. 60) states, " By the upturning of the outer demibranch, three surfaces become one with corresponding lessened risk of choking the gill and with much greater efficiency of transport and sorting of material upon it ". These relations, as noted by Yonge, are adaptations for the handling of large quantities of small particles carried into the mantle cavity from the muddy substratum. Large complex ctenidia would create strong respiratory currents through the ctenidial pores which would tend to be clogged by these particles. Small ctenidia with lessened respiratory currents are not so likely to be choked.

Large palps present an increased selective area and are required for the sorting of large amounts of incoming material.

A further adaptation to deposit feeding found in the Tellinacea is the presence of special cirrus-like cilia on the inner demibranchs (Atkins, 1937, pp. 360–370). These cilia function in three concomitant ways : (1) by increasing the strength of the incurrent flow to overcome the resistance of the elongated incurrent siphon (stressed by Atkins, 1937, p. 367) ; (2) by leading incoming deposits quickly past the ctenidium to the palps, thus preventing clogging (stressed by Yonge, 1949, p. 60) ; and (3) by increasing the strength of the incurrent flow to facilitate uptake of deposits from the environment.

Acila and *Nucula* seem to be adapted for the handling of large quantities of particulate matter received through the incurrent opening from a muddy environment in much the same way as are certain of the Tellinacea, although specific adaptations towards meeting the problems of living in such an environment differ. Below, in the left-hand column of Table 2, the *general* adaptations

Table 2—Features shared by *Acila castrensis* and *Macoma balthica* as adaptations for deposit feeding in muddy environments.

General adaptation	*Acila* (specific adaptations)	*Macoma* (specific adaptations. Information from Yonge, 1949)
I. Incurrent opening in close contact with substratum	Incurrent opening just below surface of substratum	Elongated incurrent siphon capable of sweeping surface of substratum
II. A strong incurrent for picking up deposits	Created by ciliation of outer surfaces of outer palp lamellae and of mantle	Created by cirrus-like cilia on inner demibranchs
III. Incoming deposits directed to palps and not to ctenidia	Ciliation of palp and mantle surfaces intercepts *most* particles *before* they reach ctenidia	Cirrus-like cilia on inner demibranchs create a strong current directing deposits past ctendia and towards palps
IV. Adaptations of the ctenidia for the prevention of clogging of interfilamentary spaces	1. Weak currents of the lateral cilia of ctenidial leaflets unable to draw any but the smallest particles to ctenidial surfaces	1. Cirrus-like cilia carry deposits quickly past ctenidia to palps
	2. Small ctenidia with uncomplicated demibranchs; exposed ctenidial axis creates a simple surface	2. Small ctenidia with reflexed and reduced outer demibranchs ; exposed ctenidial axis creates a simple surface
	3. Frontal cilia remove particles that have reached the ctenidia	3. Frontal cilia remove particles that have landed on the ctenidia
V. Large complex areas for rigorous sorting of deposits	1. Large, extremely complex palp lamellae with a variety of ciliary tracts	1. Large palp lamellae
	2. Complex contours of folds of the lamellae	2. Complex contours of folds of the lamellae (Fig. 11)

of the ctenidia and of the palps to deposit feeding in muddy bottoms are listed for *Acila castrensis* and *Macoma balthica*. The specific method or organ employed in carrying out the general function is given under the name of the organisms. In addition to the similarities of the organs of feeding, the stomachs of protobranchs and tellinaceans bear likenesses to one another. These are discussed by Yonge (1949).

Yonge (1949, p. 31) used " deposit feeding " in a broad sense to indicate the source of food utilized by the Tellinacea, the Nuculidae, and the Nuculanidae. In the latter two groups, the palp proboscides alone were considered to be feeding structures. From the preceding discussion in the present work, it can be seen that " deposit feeding " by removal of particles from the incurrent water differs greatly from " deposit feeding " via the palp proboscides where particles gathered do not *ever* enter into suspension within the mantle cavity. In actuality, removal of deposit particles from the incurrent water is not essentially different from suspension feeding, although requiring special adaptations for the handling of large masses of incoming material. In order to distinguish between these two types of deposit feeding, it is proposed that " inhalant deposit feeding " refer to the type of feeding observed in the Tellinacea and in the Nuculidae, wherein particles are removed from a suspension within the mantle cavity, and that " proboscidial deposit feeding " refer to the type of feeding in which the palp proboscides lead mucous masses directly to the palp lamellae. Both methods of feeding are employed by the Nuculidae. Particles utilized by *Acila* seem always to have their source in bottom deposits.

The Nuculidae with reference to early evolution of the Bivalvia

A generally held conception is that conditions in the Nuculidae " . . . probably correspond fairly closely with those of the primitive Lamellibranchia from which the existing higher forms evolved." (Yonge, 1939, p. 144.) On the basis of the facts as they were then known, Yonge (1939) proposed that organs functionally resembling palp proboscides were the feeding structures of the ancestral bivalves and that palp lamellae were developed later as sorting devices. There was a transference of feeding from the palp proboscides to the ctenidia during the evolution of lamellibranchiate forms from the deposit feeding ancestors. This transference led to the loss of the primitive proboscis-like appendages, the lamellae being retained as the labial palps of lamellibranchiate bivalves. Yonge has maintained (p. 135) that the presence of proboscides in Recent forms ". . . indicates that the Lamellibranchia *must* have passed through an evolutionary stage corresponding to the condition exhibited by the modern Nuculidae." He has further stated that support for this hypothesis must ". . . depend largely upon its inherent probability." (Yonge, 1959, p. 211). This scheme is re-examined in light of new discoveries.

Observations reported in the present paper suggest that the Nuculidae feed not only by means of the palp proboscides as thought by Yonge, but also significantly by means of the outer surfaces of the outer palp lamellae and by an hitherto unsuspected morphological and functional association of the ctenidium and palp. Thus the Nuculidae are suspension feeders (or are

inhalant deposit feeders as the term is used in this paper) as well as proboscidial deposit feeders. The relative importance of these modes of feeding is unknown. *A priori*, to agree with Yonge's opinion that the proboscides are the major organs of feeding in this family would seem reasonable, for their highly developed nature indicates that they are of great importance in this group. Also, the character of the gizzard-like stomach indicates that coarsely grained deposited material does enter this organ in quantity. But if conditions in the Nuculidae reflect the nature of earlier " transitional " types, one may wonder whether these earlier bivalves were proboscidial deposit feeders *and* suspension feeders as are the Nuculidae, or whether one mode of feeding was predominant. The following facts and the implications derived from them may aid in determining the significance of the protobranch organs of feeding in the early evolution of the Bivalvia.

That no family of protobranchs with Recent members gave rise to filibranchs and eulamellibranchs seems certain. The Nuculidae did not arise until the Late Ordovician (Deschaseaux, 1952, p. 271). *Nucula* s.s. first appears in Devonian rocks (Dechaseaux, 1952, p. 262), and *Acila* ranges from the Cretaceous (Schenck, 1943, p. 67). The Ctenodontidae, first appearing in the Late Cambrian (Dechaseaux, 1952, p. 226), probably gave rise to the Nuculidae, the Nuculanidae, and the Malletiidae (Cox, 1959), and appear earlier, geologically, than certain other bivalve groups probably ancestral to the majority of extant bivalves (Douvillé, 1912 ; Newell, 1954 ; Soot-Ryen, 1955 ; Cox, 1959). There are, however, no " connecting links " between the Ctenodontidae and these other bivalves to show that the latter were derived from the former (cf. Douvillé, 1912 ; Cox, 1959). The Ctenodontidae probably possessed the " primitive " characters of existing protobranchs as summarized by Yonge (1939, p. 141). The paleontological evidence indicates that the Nuculidae and the other named groups of Recent Protobranchia are a side branch in evolution quite apart from that giving rise to lamellibranchiate forms. This view is supported by the work of Owen (summarized, 1959) who has stated (p. 222) that " . . . the specializations of the digestive system in the Nuculacea suggest that it is unlikely that they give rise to other members of the Bivalvia. . . ."

Among extant bivalves palp proboscides appear only in the Protobranchia. There appear to be no structures homologous with these organs in any lamellibranchiate form at any stage in development. Drew (1901) has shown that the palp pouch and the palp proboscis each represent a pair of hypertrophied folds of the lamella with a sulcus remaining between the folds. The palp proboscis represents the penultimate pair of folds, and the palp pouch the last pair. Both structures are found on the outer palp lamella only and form, in conjunction with the first few folds and sulci, an intricate and highly specialized functional unit. The palp proboscis and the palp pouch begin their differentiation well after the palp lamellae are recognizable as definite, probably functional, structures in a ciliary-feeding organism. The young of the two divergent lines of evolution resemble each other in the presence of palp lamellae and of suspension feeding. One is reminded of von Baer's observation

(well summarized by de Beer, 1958) that younger stages of related forms more closely resemble one another than do later stages or adults.

The above evidence may be summarized as follows : The Nuculidae have not given rise to lamellibranchiate bivalves. The young bivalved stages of the Nuculidae are most probably suspension feeders (cf. Yonge, 1959, p. 211). At any rate they obtain food in the absence of palp proboscides which appear in the existing Protobranchia as unique specializations of pre-existing palp lamellae. The adults of the modern Nuculidae retain the ability to remove particles from an incurrent stream of water.

From the theoretical standpoint there is the suggestion that the young of the bivalves ancestral to both major groups discussed here possessed palp lamellae and were suspension-feeders and that they maintained at least some suspension feeding when adult. It may be that as adults they possessed palp proboscides and that through time they gave rise, directly, to existing protobranchs, and, by paedomorphosis, to lamellibranchiate bivalves. Yonge (1959) has supported this view.

An alternative view is that the ancestral bivalves were mainly suspension-feeders throughout their life history and that palp proboscides were absent. A restricted group (possibly the Ctenodontidae) became adapted, as adults, for gathering deposits via secondary modifications of the outer palp lamellae. These modifications gave rise to the palp proboscis and palp pouch of modern protobranchs. Having thus entered into unexploited environmental niches, these forms diversified into the successful array of protobranchiate types now extant. A second evolutionary trend leading to modern lamellibranchiate forms involved enlargement and specialization of the ctenidia as the main food collecting organs.

Which if these views is the more nearly correct can not be said on the present state of our knowledge. The existence of proboscides in Recent protobranchs clearly cannot be evidence that like organs were present in the ancestors of lamellibranchiate bivalves. The existence of suspension-feeding in the young of *Nucula* suggests that the development of palp proboscides is not an essential preliminary to life within the bivalved shell. Therefore, in the absence of any theoretical necessity to do so, it seems to the present investigator superfluous to imagine that the ancestral bivalves possessed proboscides. It is suggested that Yonge's concept be modified to read, "Conditions in the young of the Nuculidae and of lamellibranchiate forms probably correspond fairly closely with those of the young of the hypothetical primitive Lamellibranchia from which the existing higher forms evolved. As the young bivalved organisms were probably able to feed upon suspended material, there is no need to postulate the presence of palp proboscides in the adult forms of the ancestral bivalves."

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KEY TO THE LETTERING OF FIGURES

A	Anus
AA	Anterior adductor muscle
AC	Line of attachment cilia on outer demibranch
AF	Acceptory flap
C	Ctenidium
CD	Crypt depositional zone
CT	Ciliary tuft
DG	Distal oral groove
F	Foot
FC	Cleft of foot
FK	Keel of foot
IL	Inner palp lamella
LC	Opening into lamellar crypt
LDR	Lamellar division ridge
LG	Lateral oral groove
M	Mouth
MA	Mantle (folded back)
MT	Major tract of proboscis
OD	Outer demibranch
OL	Outer palp lamella
OT	Outwardly beating tract of proboscis
PA	Posterior adductor muscle
PF	Posterior folds of the lamella
PI	Massing area or " pit " of palp pouch
PO	Palp pouch
PP	Palp proboscis
PR	Turning point of tracts 9
RG	Reception grooves or functional extensions of the lateral oral groove
RP	Rejection point of palp lamella
SM	Suspensory membrane of palp
VS	Ventral rejectory shelf
VSI	Ventral rejectory shelf of inner lamella
VSO	Ventral rejectory shelf of outer lamella
X	Point where line of enlarged frontal cilia ends

THE EXTERNAL APPEARANCE AND SYSTEMATIC POSITION OF *GOBIUS FORSTERI* (TELEOSTEI-PERCOMORPHI)

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[Accepted 14th February 1961]

(With 6 figures in the text)

The object of this paper is to redescribe *Gobius forsteri* Corbin 1958, and to determine the systematic position of this species. Study of the distribution of the lateral line sensory papillae in particular has indicated that *G. forsteri* belongs to the subgenus *Zebrus* De Buen 1930, where it may be identical with *G. thori* De Buen 1928.

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INTRODUCTION

In the course of an aqualung investigation into the zoology of sublittoral rocky areas near Plymouth, Mr G. R. Forster, of the Plymouth Laboratory, obtained specimens of a goby previously unknown to the British fauna. A report on this fish was published by Corbin (1958) who proposed the new specific name of *forsteri* for the goby and placed the species within the genus *Gobius*. Apart from details of coloration and some meristic data, Corbin's description contained only brief references to those morphological characters most involved in gobiid classification, and the purpose of this redescription is to make good these deficiencies so that the systematic position of *G. forsteri* can be properly assessed. No holotype was indicated by Corbin, so that nine fishes specified in his text must be regarded as syntypes of *G. forsteri*. Through the kindness of Mr Forster, I have been able to examine two Plymouth specimens, one of which may be a syntype. Uncertainty over this matter, however, has prevented me from regarding this fish as a lectotype, and it is to be hoped that lectotypes will be designated and made available for study by the original author.

In gobiids, the lateral line system consists of cephalic canals, somewhat reduced in extent and usually opening to the surface by pores at fixed positions, and sensory papillae, comparable to canal neuromasts of less specialized fishes and distributed in definite though complex patterns over the head and body surfaces. Sanzo (1911), in a comparative investigation of their disposition

and innervation, found that study of the arrangement of these pores and papillae was of great value in the elucidation of taxonomic relationships among the European gobies. His work has been amplified by other Mediterranean ichthyologists, notably F. De Buen, whose classification (1930) of the European Gobiidae remains the most modern general treatment. Although this approach has been largely neglected by more northern workers on European fishes, the undoubted importance of these patterns makes a detailed account of them essential in any taxonomic description of a goby, and explains the somewhat lengthy section devoted below to their examination.

DESCRIPTION

Gobius forsteri Corbin (Fig. 1)

Gobius sp., Marine Biological Association (1957), p. 400.
Gobius forsteri, Corbin (1958), p. 1659 ; Hardy (1959), p. 212, & plate 3.

Material

The following description is based on three examples. These include a male (British Museum No. 1960. 7. 27. 1.) of standard length 83+ caudal fin length 17·5 mm. from Tinker Shoal, outside the main Plymouth breakwater, and a female (B.M. No. 1960. 7. 27. 2.) of 85+? mm., probably from Queener Point, Whitsand Bay, near Plymouth. The latter specimen may be one of the syntypes of this species. Both the localities mentioned were described by Forster (1958). The third example, an immature male of 41·5+11·5 mm., was collected by Professor E. W. Knight-Jones when diving at Dale Fort, Pembrokeshire (South Wales), in August 1960.

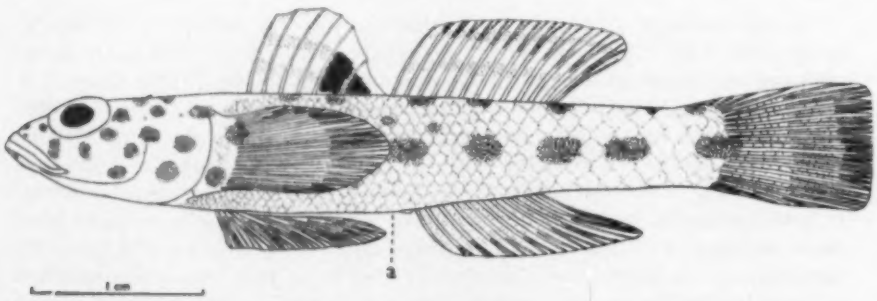

Fig. 1—*Gobius forsteri* Corbin. Immature male from Dale Fort. a=position of anus.

General description

Body subcylindrical, laterally compressed towards caudal fin ; in standard length, depth at origin of pelvic fin 4·9–6·1, at origin of anal fin 6·2–6·4, of caudal penduncle 9·2–10·1. Head large, rounded ; in standard length, horizontal length (snout to upper origin of opercle) 3·6–3·8, maximum width (between upper origins of opercles) 6·1–7·5, depth behind eyes 6·4–7·2. Horizontal distance from tip of snout to origin of first dorsal fin 2·8–3, to anus (and origin of second dorsal fin) 1·8–1·9, to origin of pelvic fin 3·3–3·5, all in standard

length. Caudal peduncle (end of anal fin base to origin of caudal fin) horizontal length 4·3–4·6 in standard length, depth 2–2·4 in own length. In head length, snout 4·6–5·2, eye 3·5–3·6, postorbital length 1·9–2, upper jaw 1·9–2·7, cheek (lower border of orbit to posterior end of upper jaw) 3·5–5·4 (eye, upper jaw, and cheek direct, rest horizontal measurement). Interorbital minimum width, fleshy 2·6–5·7, bony 8·3–14·2, in eye length. Snout less than diameter of eye, with profile moderately sloping ; anterior nostril on short tube, not projecting beyond upper jaw and with entire distal rim without local prolongation ; posterior nostril a slit on minor prominence. Eyes relatively large, close together. Postorbital profile more or less flat. Mouth somewhat oblique, lower jaw slightly in advance of upper ; maxilla ends posteriorly under anterior third of eye. Villiform teeth form narrow band on each jaw, with outer and inner rows of more dispersed, rather larger, caniniform teeth. Tongue truncate, with very slight emargination of anterior border. Branchiostegous membrane attached along entire border of isthmus. Vertebrae (including urostyle) 28.

Fins

Comparison of second dorsal and anal fin-ray counts with those of Corbin (1958) would seem to indicate that in the original description the first spinous ray in these fins was not distinguished from the remaining articulated rays, and that the last ray in both fins, which is bifid to the base, was counted as two. In the method adopted here for recording fin-ray numbers, spinous elements are represented by large roman, branched articulated by arabic, and unbranched articulated by small roman numerals. The terminal bifid ray in the second dorsal and anal fins is regarded as one ray, and only branched rays counted for the caudal fin. Values given by Corbin for first and second dorsal and anal fins, converted to the system followed in this paper, are cited in brackets.

First dorsal fin VI–VII (V–VII) ; second dorsal I, 11–12 (I, 11–12) ; anal I, 10 (I, 10) ; caudal 13–14 ; pectoral i, 16–18 ; pelvic I, 5. In standard length, first dorsal base (VI) 8·3–8·7, (VII) 6·8 ; second dorsal base 3·8–4·2 ; anal base 5·4–5·9 ; longest caudal ray 4·6–4·75 ; longest pectoral ray 4·4–5·1 ; pelvic origin to posterior rim of disc 4·2–4·25 (fin base lengths direct, between origins of first and last elements). First dorsal fin begins above or just behind vertical of pelvic origin ; last ray arises well before vertical of anus. Length of longest first dorsal ray about two-thirds depth of body at origin of pelvic fin ; none of first dorsal rays markedly produced beyond border of fin membrane. Slight dorsal interspace present. Second dorsal fin begins over anus ; base finishes above or shortly behind vertical of end of anal fin base. Margin of second dorsal damaged in larger specimens ; in smallest fish, about as high as first dorsal, with posterior angle rounded and reaching rather more than half-way to origin of caudal fin. Anal fin commences a short distance behind anus, below second or third branched rays of second dorsal fin, and ends below or slightly in advance of posterior end of second dorsal base. Posterior corner of anal fin produced, moderately acute, with penultimate (longest) ray almost equal in length to anal base, and two-thirds to three-quarters length of caudal peduncle. Caudal fin with rounded margins ; posterior edge slightly convex.

Pectoral fin extends back to vertical of posterior end of pelvic disc, short of anus, or to opposite the anus in smallest fish. No trace of separation of uppermost pectoral rays from fin membrane. Pelvic disc entire ; anterior membrane well developed, moderately deep, with straight free edge having inconspicuous minute lateral lobe about distal termination of each spine ; articulated rays much branched, their wide distal ends adjoining to form finely crenate margin of disc. Pelvic fin ends at anus in smallest fish ; short of anus in larger, with fin length 1·2 in distance from pelvic origin to anus.

Scales

Body entirely covered by moderately large, imbricating, ctenoid scales, in lateral series 36–38 (34–38, Corbin, 1958), and in transverse series (anterior end of second dorsal fin backwards to anal fin) $\frac{1}{2}$, 10–11, $\frac{1}{2}$. Scales absent from head, including opercle, and predorsal region before line connecting upper end of pectoral base with origin of first dorsal fin ; also lacking on narrow strip flanking base of first dorsal fin, in axilla, on much of anterior and all posterior face of pectoral lobe, and on anterior half of isthmus. Pseudocycloid scales on posterior part of isthmus, breast, and midventral line, and in small patch on anterior face of pectoral lobe. Scales largest on caudal peduncle, up to more than twice size of those below first dorsal fin, roughly hexagonal, deeper than long, with focus near posterior angle (more acute than anterior) ; in larger fish, 20–35 radii on anterior region, and 55 to over 85 closely set, moderately elongate ctenii on posterior edge of scale.

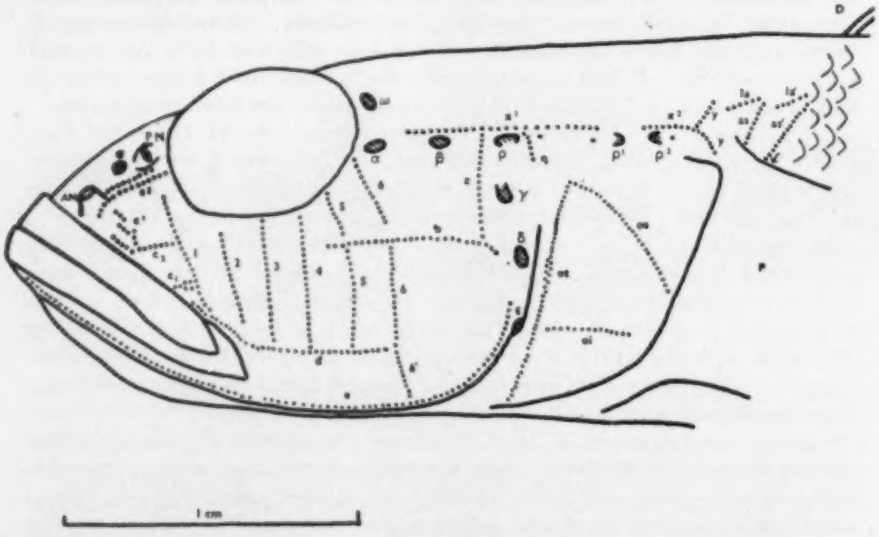

Fig. 2—Diagram of cephalic pores and sensory papillae on head of *G. forsteri* in lateral aspect. Numbers of papillae in rows are intermediate between extreme values for the larger fishes. Papillae black; pores cross-hatched ; AN, anterior nostril ; PN, posterior nostril ; D, origin of first dorsal fin ; P, pectoral fin ; other letters referred to in text.

Lateral line system (Figs. 2 and 3)

Letters in the accompanying diagrams and terminology of the various canals and papilla series in the present text are those proposed by Sanzo (1911) except when otherwise stated. Superior or inferior marks against letters used by Sanzo to denote subdivisions of particular series have been replaced by appropriate roman numerals in the same position. The sensory papillae of the larger male were brought into relief by the staining technique of De Buen (1923). Counts of papillae in the smallest specimen are provided in brackets when these are appreciably outside the range of those in the larger fishes.

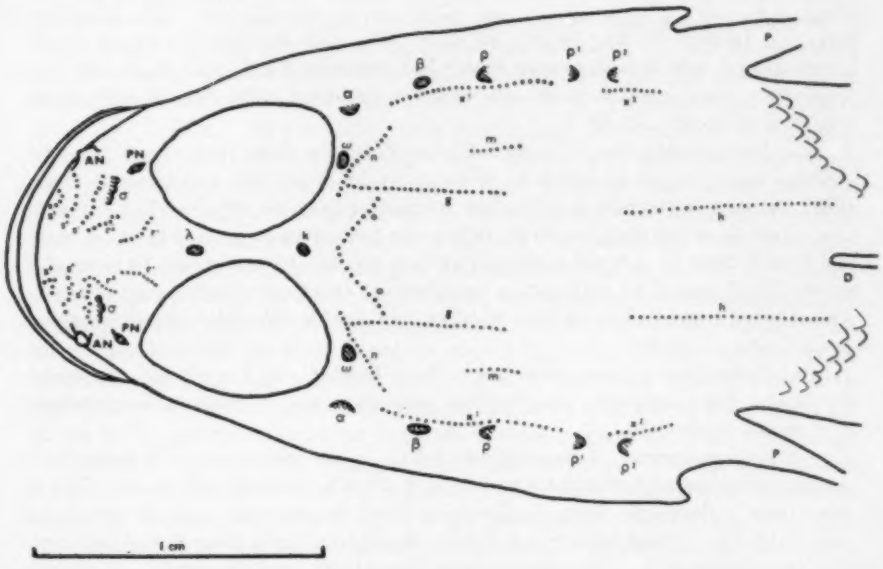

Fig. 3—As Fig. 2, dorsal aspect. A symmetrical arrangement is not adopted, since minor discrepancies may occur between opposite sides of actual specimens.

Cephalic canals

Anterior and posterior oculoscapular, and preopercular canals present with full complement of pores—σ, λ, κ, ω, α, β, ρ ; ρ^1, ρ^2 ; and γ, δ, ϵ respectively. Posterior oculoscapular canal short, ρ^1 widely separated from ρ by much more than length of posterior oculoscapular canal.

Sensory papillae

(i) Preorbital. Median internal series r in two rows ; posterior (r^1) 6–10 papillae, anterior (r^2) 5–9. Median external series s in three transverse groups ; posterior (s^1) 6–11, middle (s^2) 4–10, anterior (s^3) 4–6. Lateral series c in three parts ; superior (c^2)in two longitudinal rows, upper 6–10, lower 13–16 (8–9) ;

middle with horizontal row (c_2) 9–14 and vertical tract (c^1) 6–12 ; and inferior (c_1) 3–7.

(ii) Suborbital. Without row *a* along lower border of orbit ; six transverse rows (*1, 2, 3, 4, 5, 6*) with rows *5* and *6* separated into two parts by longitudinal row *b*. Inferior limb of row *6* continued (as 6^1) below origin of row *d* across lower part of cheek to vicinity of external preopercular-mandibular row *e*. Counts of papillae are :—

row	*1*	*2*	*3*	*4*	*5* sup.	*5* inf.	*6* sup.	*6* inf.	6^1
large fishes	19–22	17–21	19–21	22–25	10–11	15–18	11–18	15–19	8–16
small fish	19–20	17–18	16–17	16–18	9	10–11	14–18	11–12	6–10

Longitudinal row *b* commences somewhat anterior to δ, and ends between transverse rows *4* and *5*, or in one instance against *5* ; 25–33. Longitudinal row *d* continuous, 33–38.

(iii) Preopercular-mandibular. External row *e* from just above level of ϵ along lower border of cheek to articulation of lower jaw and forward along ridge flanking inner side of lower jaw to mental area, 81–88 (74–77) ; internal row *i* (not shown in diagram) from below ϵ in preopercular groove to jaw articulation and then to mental region in groove median to row *e*, 32–39 ; mental series *f* (not shown in diagram) a longitudinal tract on anterior part of intermandibular muscle, close to that of other side, backwards from anterior ends of rows *i* and *e*, 18–27.

(iv) Opercular. Transverse row *ot* from behind γ to lower edge of opercle, 46–54 (34–35) ; superior longitudinal row *os*, 24–27 ; inferior longitudinal row *oi*, 13–14 (9–10).

(v) Oculoscapular. Longitudinal series *x* in two rows ; anterior (x^1) commencing between verticals of α and β, 21–27, posterior (x^2) 7–13. Transverse row *z* descends from x^1, finishing close to posterior end of suborbital row *b*, 16–20. Transverse row *q* 4–10. No sign of transverse row above level of x^1 in vicinity of ρ. Transverse row *y* above upper end of opercle, upper limb 7–10, lower 6–10. On level of pores, one or two papillae occur behind upper end of *q*, one or two below last papilla of x^1, and one below middle of x^2 posterior to ρ^2. Only two axillary series, each with upper longitudinal and lower transverse component ; anterior longitudinal (*la*) 5–10, posterior longitudinal (la^1) 5–9 ; anterior transverse (*as*) 8–13, posterior transverse (as^1) descending into upper part of axilla. 20–22 (14–17).

(vi) Anterior Dorsal (Occipital). Transverse row *n*, 11–18. Longitudinal row *g* elongate, meeting anterior end of *n* behind border of orbit, 20–26 (15–18). Transverse row *o* curves forwards to midline from inner side of anterior quarter of *g*, 9–10. Median end of row *o* lies immediately behind or in front of that of other side, or joins fellow in midline. Longitudinal row *m* developed, 7–10. Longitudinal row *h*, 25–32.

(vii) Trunk and Caudal. Not shown in diagram, and not studied in detail ; appear to present no unusual features. Include transverse row from base of first dorsal fin opposite third or fourth ray, 9–13 ; longitudinal series of more

than twenty short transverse rows along midline of body ; and longitudinal rows on three caudal branched rays.

Coloration

Of the living fish, Corbin (1958) remarks that " its colouring is surprisingly brilliant and arresting : large and conspicuous bright orange or brick-red spots are evenly disposed in a regular pattern on a pale straw-brown ground colour. On the nape, midway between the eyes and the first ray of the first dorsal, is a large orange spot ringed by eight others, four on each side of the midline. Continuing towards the tail, other pairs flank the dorsal fins and there are six large orange spots on the sides of the body . . . . . with smaller intermediate ones. On the dorsal fins there are longitudinal bands and spots of this orange and the hind part of the first dorsal is black . . . . During courtship and incubation the colouring of the male is intensified and the ground colour darkens almost to a black-purple." Hardy (1959) provides a coloured illustration of *G. forsteri*. All the material at my disposal was preserved in formalin. The two large examples are generally a light brown, with scales edged in black. Along the lateral midline are indistinct dark blotches—one under the first dorsal fin, one below the origin of the second dorsal fin, and two or three between this and the last one at the origin of the caudal fin. On the nape, large oval patches with pale margins and dark centres appear to correspond with orange spots of the original description, and when first examined contained vestiges of this colour. In the first dorsal fin, the lower two-thirds of the membrane between the fifth and sixth rays is black, as in the posterior membrane of this fin. The smallest specimen is a pale grey brown, with dark blotches ; comparison of the disposition of the latter with colour transparencies of the living animal shows that these dark areas correspond with the orange blotches forming this species' most obvious characteristic. The arrangement of these on the nape agree exactly with Corbin's (1958) description. Six large orange spots along the lateral midline are identical in position with the dark patches shown in the larger preserved examples. Elsewhere, on the head, orange markings occur on the snout, cheeks, and opercles, between the eyes and, more faintly, in the mental region. Along the back, two and three spots flank the bases of the first and second dorsal fins respectively. Several smaller blotches are scattered between these and the midline, as well as below the latter. In addition to the conspicuous black marking on the first dorsal fin, the dorsal fins carry two narrow longitudinal bands of orange. Vertical orange striae occur on the caudal, but the pectoral, pelvic, and anal fins appear to lack this pigmentation save for two orange spots found on the lobe of each pectoral fin.

DISCUSSION

Generic identification

The species described above has all the characters of the genus *Gobius* L., as defined by De Buen (1930, 1931) in terms of the lateral line system in his synopses of the European gobies. These features include the occurrence of cephalic canals and pores, with five pores (α, β, ρ, ρ^1, ρ^2) along the oculoscapular

groove and three (γ, δ, ϵ) on the preopercular canal but with the absence of interorbital longitudinal series of pores. There are on each side of the head at least four median preorbital rows of sensory papillae, four entire transverse suborbital rows followed by two divided by a longitudinal row (*b*), and neither a longitudinal suborbital row (*a*) immediately below the eye nor tranvserse rows between the eyes.

Intrageneric relationships

The European representatives of the genus *Gobius* were provisionally divided into twelve subgenera by De Buen (1930). In the median position of papillary row *o* with relation to row *g*, the transverse union of row *o* with its fellow from the opposite side, and the relatively low number of scales, *G. forsteri* clearly belongs to the subgenus *Zebrus*, to which De Buen allocated the Mediterranean *G. zebrus* Risso and *G. thori* De Buen. Sanzo (1911) associated *G. zebrus* with *G. quadrivittatus* Steindachner (=*G. depressus* Kolombatovic) but for the latter species De Buen erected another subgenus, termed *Chromogobius*, characterized by a high number of scales in conjunction with a relatively shorter anal fin. As shown by Sanzo (1911), there is a median union of rows *o* in *G. quadrivittatus* although this was not mentioned by De Buen. It is convenient to discuss the relationships of *G. forsteri* with *G. zebrus* and *G. quadrivittatus* before proceding to compare *G. forsteri* with *G. thori*. In doing this, reliance has been placed on published descriptions and examination of some *G. zebrus* and *G. quadrivittatus* collected by Mr A. C. Wheeler on the Spanish Mediterranean coast.

In patterns of sensory papillae, *G. zebrus* differs greatly from *G. forsteri* in the constant possession of an additional short transverse suborbital row between row *6* and pore α; the shortness of row *g*, which does not run forwards beyond the lateral end of row *o* and whose anterior end is quite distant from row *n* ; the wide separation between row *z* and the posterior end of row *b* ; the origin of row x^1 behind the vertical of pore β ; and the absence of row 6^1 and the anterior median internal preorbital row r^2. *G. quadrivittatus*, on the other hand, closely resembles *G. forsteri* in some aspects of the lateral line system. The most notable similarities are the presence of row 6^1 (not shown by Sanzo, 1911, and possibly variable in *quadrivittatus*), and the forward extension of row *g* anterior to the lateral termination of row *o*. The possession of an additional suborbital transverse row, and only one median internal preorbital row (r^2), together with the separation of rows *z* and *b*, differentiates *G. quadrivittatus* from *G. forsteri* and recalls *G. zebrus*, but the extra suborbital row appears to be of rather variable occurrence, and in the origin of row x^1 over pore β *G. quadrivittatus* approaches *G. forsteri*. Reduction or loss of row *m* and of the posterior oculoscapular canal are features peculiar to *G. quadrivittatus*.

In other anatomical characters, *G. forsteri* is distinguished from *G. zebrus* and *G. quadrivittatus* by the presence of scales on the isthmus, and the absence of free superior pectoral rays. A small tentacle on the rim of the anterior nostril of *G. zebrus* is unrepresented in the other two species, and *G. forsteri*

does not have the posterior nostril prolonged into a short tube like that of *G. quadrivittatus*. Lateral lobes on the anterior pelvic membrane, minute in *G. forsteri*, are well developed in *G. quadrivittatus*, but absent in *G. zebrus*. In other aspects of body form, *G. forsteri* appears closer to *G. zebrus* than to *G. quadrivittatus* which has a much shorter pelvic fin, wider interorbital space and smaller eyes. *G. forsteri* has rather more rows of scales (34–38) than *G. zebrus* (28–34), but far fewer than *G. quadrivittatus* (about 60) ; both the latter species have slightly fewer fin rays in the second dorsal (10–11) and in the anal (8–10 and 9), when compared with *G. forsteri* (12–13 and 11 including spinous rays). In two respects *G. forsteri* stands quite apart. Its coloration is entirely unlike those displayed by *G. zebrus* and *G. quadrivittatus*, where the main pattern consists of vertical bars. There is also a comparable separation in maximum size ; neither of the latter species exceeds 60 mm., while *G. forsteri* reaches 120 mm., (Corbin, 1958).

To conclude, it would appear that no closer relationship can be found between *G. forsteri* and *G. zebrus* than between the former and *G. quadrivittatus*, when only the usual anatomical characters are taken into consideration. However, a distinct affinity between *G. forsteri* and *G. quadrivittatus* is suggested by the occurrence in both of two peculiarities in the distribution of the sensory papillae (row 6^1, and anterior prolongation of row *g*) which are not seen together in any other European gobies, including *G. zebrus* but excepting *G. thori*. As set out below, *G. thori* and *G. forsteri* are very much alike in many features, and, since De Buen (1930) was satisfied that *G. thori* could be placed in his subgenus *Zebrus*, this agreement between *G. forsteri* (and *G. thori*) on the one hand, and *G. quadrivittatus* on the other, seems to denote a more pronounced connection between the subgenera *Zebrus* and *Chromogobius* than De Buen allowed. Although a considerable amount of taxonomic effort has been expended on the systematics of European gobies, a good deal remains to be accomplished, not only through study of the lateral line organs but also by close attention to general morphological detail.

Affinities with G. thori

De Buen (1928) founded a new species—*G. thori*—on a description by Fage (1918) of an Aegean goby identified by the latter as *G. zebrus*. De Buen clearly enumerated the differences between the true *G. zebrus* and Fage's single specimen, which De Buen took to represent a previously unnamed species. Comparison of *G. forsteri* with *G. thori*, as far as the original description will permit, indicates that these species are very intimately related. Inspection of Fig. 2 and 3 with 4 and 5 will reveal that they have in common a long row *g*, enclosing the united rows *o* and ending anteriorly at row *n* ; the suborbital row 6^1 ; the proximity of the lower end of row *z* to the posterior end of suborbital row *b* ; and an anterior median internal preorbital row r^2, in addition to the posterior r^1. The only important differences in the arrangement of the papillae are the more posterior origin of x^1 in *G. thori* (behind vertical of β) and some dissimilarity in the more posterior section of the oculoscapular series. In *G. thori* (Figs. 4 and 5, from Fage, 1918), there is a short longitudinal row under the posterior end of x^1 ; a few transverse papillae at the posterior end of x^1 (*tr*) ; reduction

of y to one papilla ; and an additional axillary transverse series (*as*). However, in *G. forsteri*, a papilla occurs under x^1 behind y, and one or two papillae lie transversely below the posterior end of x^1, while the single papilla noted under x^2 could represent the papilla y in Fage's figure of *G. thori*, and the transverse row y the first transverse axillary row *as* of *G. thori*.

The number of papillae comprising the various rows in *G. forsteri* does not differ consistently with length of fish in my limited sample. Comparison of such counts for *G. forsteri* with numbers shown in Fage's drawing reveals a disparity which could be an important difference between the former and *G. thori*, provided that Fage intended accuracy in number as well as in arrangement of papillae. Counts mentioned in his text (row *i*, 17–18 ; row *m*, 5–6)

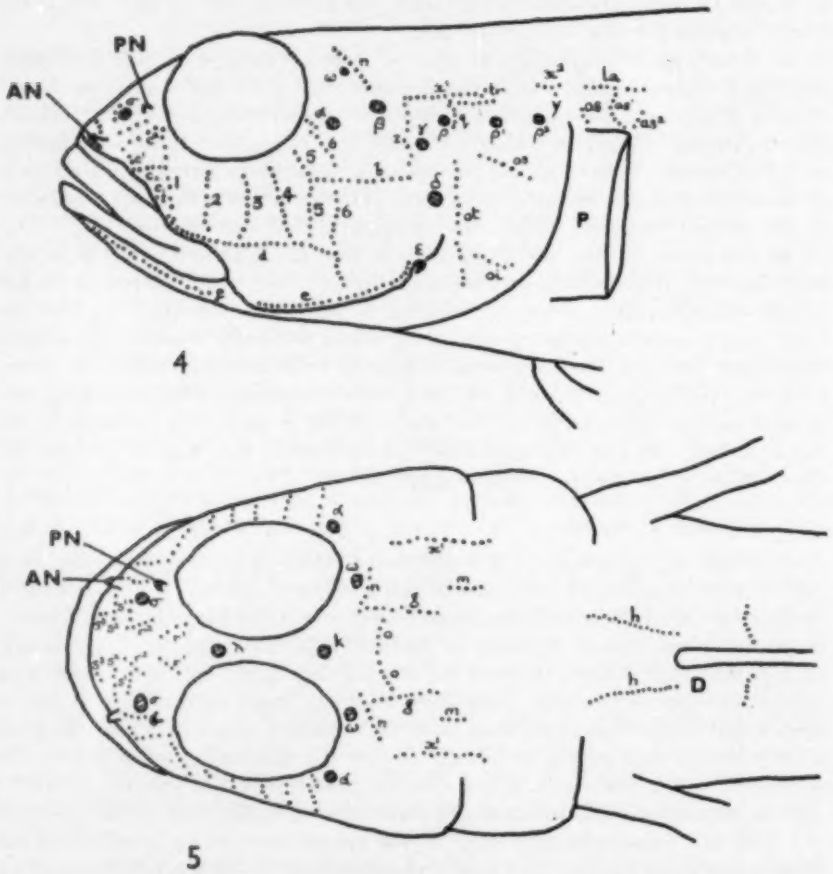

Fig. 4—Cephalic pores and sensory papillae on head of *G. thori* in lateral aspect, from Fage (1918) Lettering (slightly modified from original) as in Fig. 2.
Fig. 5—As Fig. 4, dorsal aspect.

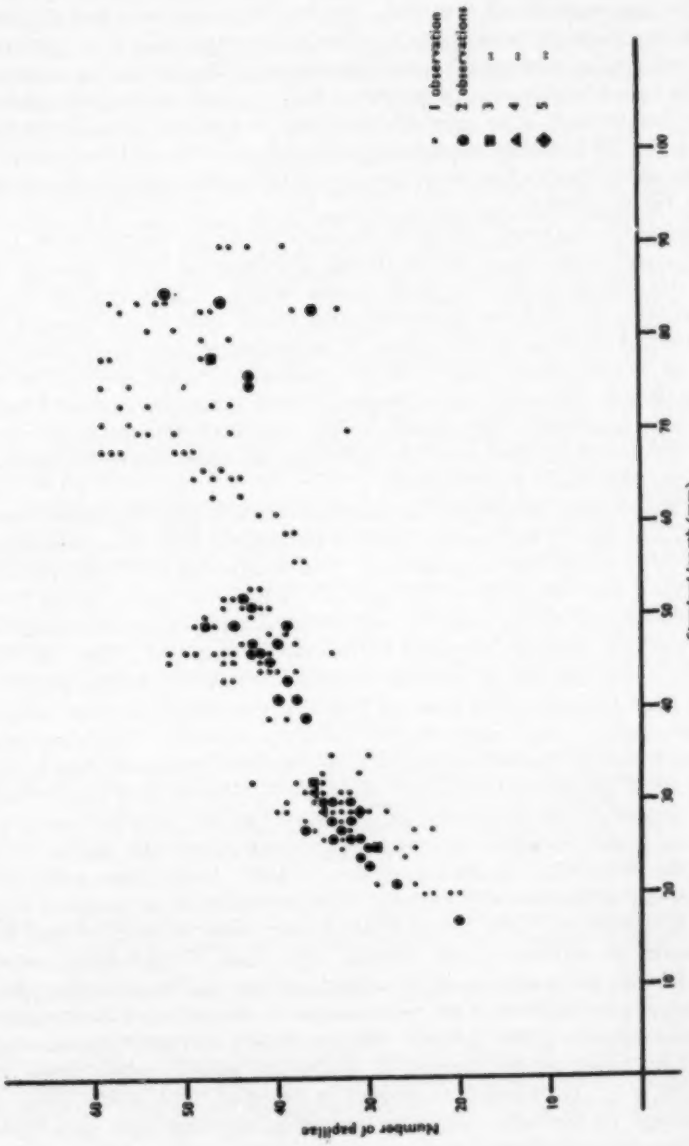

Fig. 6—Variation in number of sensory papillae in row i with length of fish in *G. paganellus* from the Isle of Man.

do indicate a smaller number than in *G. forsteri* (*i*, 32–39 ; *m*, 7–10), but a larger collection is required to test the relation between number of papillae and size of fish, and in this connection it must be remembered that the example of *G. thori* was only about four-fifths the length of the smallest *G. forsteri* examined here. In *G. paganellus* L., which is comparable to *G. forsteri* in size but belongs to another subgenus (*Macrogobius* De Buen), the number of papillae in row *i* increases with length of fish in most individuals, and at a particular length there is considerable variation in number, especially in larger fishes (Fig. 6). If a similar relation exists in *G. forsteri*, it will be apparent that the counts given for this row in *G. thori* could fall within the possible range of variation for *G. forsteri*.

The meristic characters given for *G. thori* by Fage (second dorsal I, 11 ; anal I, 9 ; and 34 scales in lateral series) are nearly or quite identical with those for *G. forsteri* (I, 11–12 ; I, 10 ; and 34–38). Unfortunately the pigmentation of *G. thori* was not described, and, in any case, the fish before Fage would have lost colour in preservation. This single specimen was " une femelle adulte " of 44 mm. total length. In *G. paganellus*, which reaches the same maximum length (120 mm.) as *G. forsteri*, ripening females may be found at half this size (personal observation), so the comparatively small size of this " adult " female of *G. thori* need not preclude the attainment of a maximum size on a par with that of *G. forsteri*.

There is sufficient resemblance in pattern of sensory papillae and in meristic characters between *G. thori* and *G. forsteri* to suggest that these names do, in fact, apply to one and the same species. The number of *G. forsteri* examined for this paper, and the single goby available to Fage, do not make up enough material to explain away the relatively minor discrepancies in papilla arrangement between the two forms in terms of individual peculiarities. The differences could be a manifestation of regional variation within one widely distributed species. Fage's account of *G. thori* omitted many points of detailed anatomy, and future work on more specimens is obviously required. The same applies to the question of relative abundance of papillae discussed above. Close correspondence, however, between *G. thori* and *G. forsteri* in so many respects seems to outweigh the maximum importance that can be attributed to the divergences so far revealed. *G. thori* was recorded from the Aegean Sea, at Station 165 (39° 48′ N, 25° 59′ E) of the " Thor " 1910 cruise, south of the Turkish island of Bozcaada (Tenedos). The extension of its range to include the area of distribution of *G. forsteri* (south-west coast of England and Wales to Santander in northern Spain, Corbin, 1958, and Knight-Jones, personal communication) need not be an argument against specific identity with the latter, since many Mediterranean species occur in the adjacent Lusitanian and Mauretanian regions of the Atlantic (Ekman, 1953), and such a wide range is paralleled by other gobies such as *G. paganellus* and *G. cobitis* Risso (=*G. capito* C. & V.). In habitat, *G. forsteri* is reported by Corbin (1958) from " rock fissures in the sides of gullies or under large boulders in a depth of between four and six fathoms on the open coast or where there are considerable reefs or precipitous cliffs ". *G. thori* was dredged from a sandy bottom at a depth of 35 metres (19 fathoms), according to the " Thor " station list provided

by Schmidt (1912). How real this ecological difference is must await further investigation.

In the absence of additional examples for study of variation, the lumping of *G. forsteri* with *G. thori* is not entirely warranted at the present time, but the very distinct possibility of their conspecificity should influence future work. In the event of this hypothesis proving correct, then the name *forsteri* Corbin 1958 would, of course, become a junior synonym of *thori* De Buen 1928.

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SUMMARY

A species of goby from the south-west coast of England and Wales, recently described by Corbin (1958) as *Gobius forsteri*, is redescribed from three specimens, with special attention paid to the configuration of the modified lateral line system. The generic identification of the species is confirmed, and its affinities with other members of the subgenera *Zebrus* and *Chromogobius* are discussed. A very close relationship is demonstrated between *G. forsteri* and *G. thori* De Buen, a Mediterranean form known from only one example, and the suggestion is made that these two species may be identical. Some differences in form and perhaps habitat prevent an unqualified affirmation of this view.

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I am very grateful to Mr G. R. Forster and Professor E. W. Knight-Jones for sending me individuals of *G. forsteri* with the relevant information, and to Messrs J. S. Colman and A. B. Bowers, of the Marine Biological Station, Port Erin, and Mr A. C. Wheeler, of the British Museum (Natural History), for helpful criticism of this paper. Professor Knight-Jones generously provided colour transparencies of the Dale Fort specimen, and Mr Wheeler kindly prepared radiographs of the larger *G. forsteri*.

SUMMARY

A species of goby from the south-west coast of England and Wales, recently described by Corbin (1958) as *Gobius forsteri*, is redescribed from three specimens, with special attention paid to the configuration of the modified lateral line system. The generic identification of the species is confirmed, and its affinities with other members of the subgenera *Zebrus* and *Chromogobius* are discussed. A very close relationship is demonstrated between *G. forsteri* and *G. thori* De Buen, a Mediterranean form known from only one example, and the suggestion is made that these two species may be identical. Some differences in form and perhaps habitat prevent an unqualified affirmation of this view.

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REPORT ON SOME MYSIDACEA FROM THE DEEPER WATERS OF THE ROSS SEA

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[Accepted 14th February 1961]

(With 10 figures in the text)

A list of species in the collection is given. Six of these are already known from the Antarctic. One species, *Hansenomysis antarctica* Holt and Tattersall, 1906, previously known only from two types and two other isolated specimens, all of which lacked the posterior region of the telson, is represented by a complete specimen and the tail-fan is fully figured and described. A species of the same genus, new to science, is described and figured; the genus is reviewed, the homology of certain organs discussed and a key for the identification of its known species given.

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Discussion on the genus *Hansenomysis* Stebbing	554
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INTRODUCTION

The material upon which this short Report is based was collected in the deeper waters of the Ross Sea by Mr John H. Dearborn and Mr Jack L. Littlepage during the Antarctic summers of 1958/59 and 1959/60. Their work was partly financed by U.S. National Science Foundation Grants N.S.F.—G–6328 and N.S.F.—G–9190. The number of specimens collected was small but they have proved to be most valuable in throwing much light on the rare and hitherto imperfectly known genus *Hansenomysis*.

The hauls were taken either in dredges or vertically from the bottom to the surface through holes blasted through the ice or through natural cracks in the ice, widened and kept open for the work. Most of the material is in unusually good condition.

LIST OF SPECIES REPRESENTED IN THE COLLECTION

Suborder MYSIDA

Family **PETALOPHTHALMIDAE**

Genus *Hansenomysis* Stebbing 1893

Hansenomysis antarctica Holt and Tattersall 1906

Hansenomysis angusticauda sp. n.

Family **MYSIDAE**

Subfamily **Mysinae**

Tribe Erythropini

Genus *Pseudomma* G. O. Sars 1870.

Pseudomma belgicae (Hansen in MS) Holt and Tattersall 1906

? *Pseudomma armatum* Hansen 1913

Tribe Leptomysini

Genus *Mysidetes* Holt and Tattersall 1906

Mysidetes posthon Holt and Tattersall 1906

Tribe Mysini

Genus *Antarctomysis* Coutière 1907

Antarctomysis maxima (Hansen in MS) (Holt and Tattersall) 1906

Antarctomysis ohlinii Hansen 1908

The type of *Hansenomysis angusticauda* is lodged in the U.S. Natural History Museum, Department of Invertebrates, Smithsonian Institution, Washington, D.C.

Suborder **MYSIDA**

Family **Pelalophthalmidae**

Genus *HANSENOMYSIS* Stebbing 1893

Arctomysis Hansen, 1887. p. 210.
Hansenomysis Stebbing 1893 p. 268.

Remarks

Four species are at present included in this genus.

1. *Hansenomysis fyllae* (Hansen) from deep waters off the south-west and south-east of Greenland, north and west of the British Isles (362–900 fms.) and from off the east coast of New England (353 fms).

2. *H. antarctica* Holt and Tattersall, 1906. Off Coulman Island in the Ross Sea, Graham Region and the North of the Bellingshausen Sea in depths between 100 and 400 m.

3. *H. falklandica* O. S. Tattersall, 1955. Off the Falkland Islands, Straits of Magellan and the Patagonian Shelf, 185–534 m.

4. *H. armata* Birstein and Tchindonova 1958. From the Kuril Kamchatka Trench in the north-west Pacific, by trawl at 2960 m.

I am now able to add a fifth species to the genus, *H. angusticauda*, of which a full description and figures appear below.

Thus the genus is widely represented in the deeper waters of the colder temperate and cold regions of the world. Records of the species have been few and, except in *H. falklandica*, the number of specimens captured has been remarkably small. In all species the integument is soft and the animals are apparently fragile, for the majority of specimens taken have been damaged, especially in the posterior region of the tail-fan, the distal end of the telson being frequently missing.

When reporting on the Mysidacea collected in the southern Atlantic and Antarctic Oceans by the "Discovery II", I, somewhat doubtfully, referred

a damaged male specimen of the genus to *antarctica* (O. S. Tattersall. 1955, p. 59), pointing out certain differences which it showed from the descriptions and figures which had been published of that species. The posterior end of the telson of the " Discovery " specimen was missing and, curiously enough, all the four specimens of *H. antarctica* which had previously been referred to the species had suffered a like mutilation. In his description of the type, W. M. Tattersall (1908, p. 23) reconstructed the telson from fragments which were found in the haul with it and he specifically pointed out that the figure which he gave of this organ was only tentative.

In the present collections there are three female specimens, as well as the abdomen and tail fan of a fourth female, which belong to the genus *Hansenomysis*. Two of the whole animals and the fragment agree so closely with the description and figures which have been published of *H. antarctica* that there can be no doubt as to their correct identity. Fortunately they are in quite good condition and in one of the whole specimens and in the fragment the tail fan is complete. It is therefore possible for the first time to describe the undamaged telson and to figure it accurately (Fig. 1).

The third specimen, which is also in fairly good condition with the telson present and only damaged slightly on one of its lateral margins, agrees with great exactitude with the damaged male specimen captured by the " Discovery I " in the Schollaert Channel, Palmer Archipelago in 1927 and referred by me (1955) to *H. antarctica*. With the complete telson of that species now available for comparison, it is quite clear that the " Discovery I " specimen and the present one belong to the same species which is new to science. To emphasise the marked difference in the form of its telson from that of *H. antarctica* I have named this new species *Hansenomysis angusticauda*. A full description of it, with figures such as can be made without dissection, is given below.

The specimens of *H. antarctica* and of the new species, *H. angusticauda* in the present collection are in such good condition that the peculiar pit-like depression on the base of each antennule with the forwardly projecting flap of tissue which partially covers it and the form of the single median eyeplate can clearly be distinguished. In the original description of *H. fyllae* no mention was made of these peculiar organs on the base of the antennules but Shen (1934, p. 536, Pl. II, fig. 15), when discussing their possible function, stated " I have confirmed Tattersall's observations in the type-specimen of *Hansenomysis antarctica* and found a very similar structure in *H. fyllae*."

Hansen's type specimen of *H. fyllae* was in very poor condition and in his original description of the species he stated that the eyes were absent. In 1908, p. 96, with better material at his disposal, he gave a very clear figure of the dorsal view of the anterior end of the animal, showing the broad, only slightly convex, anterior margin of the carapace with a triangular bluntly-rounded structure projecting forward from beneath it. He considered this structure to be the anterior part of the head. Two small, slender, forwardly-directed processes situated one on either side of the " head " were thought by Hansen to represent rudimentary eyes. In his figure the shadowy outline of the pit-like organs on the dorsal surface of the proximal region of the antennules can be seen but there is no mention of them in the text.

In the light of the much more clearly defined form of the eyeplate and of the flaps of tissue partially covering the pits on the antennules in the three Antarctic species I re-examined eleven specimens of *H. fyllae* in the collections of my late husband. These had been collected by him at various times from deep water off the west coast of Ireland. As a result of my investigations I venture to suggest that the interpretation of the form of the eyes given by Hansen, and generally accepted in the past, is incorrect. I consider that the median triangular fleshy projection which Hansen regarded as the anterior region of the head is, in fact, a single eyeplate which differs from that found in the Antarctic species only in having its anterior end produced in the median line and not into lappets on each side.

The small slender structures lying one on either side of the eyeplate which Hansen regarded as representing rudimentary eyes, are, in my opinion, the small flaps of tissue which partially cover the pit-like organs on the antennules. They are definitely not attached to the posterior edge of the pit but arise from the arthrodial membrane at the base of the antennule just at the outer end of the line of attachment of the fleshy eyeplate. The anterior margin of the head itself can be seen between the inner margins of the antennules, below the eyeplate and projecting slightly beyond it. There is a distinct furrow running vertically around the anterior end of the head so that its profile in dorsal view is markedly concave (Fig. 2).

I have not seen the type of *H. armata*. In the description and the figures given of it there is no mention of any organs on the base of the antennule. I therefore wrote to Mrs Tchindonova concerning this point and she has replied to me that similar organs to those described in other species of the genus are present. Two small slender processes occurring one on either side of a broad trapeziform structure which projects beyond and below the broadly rounded anterior margin of the carapace have been regarded by Birstein and Tchindonova as rudimentary eyes. I think that it is possible that the interpretation which I have suggested for similar structures in *H. fyllae* may apply equally well for *H. armata* i.e. the broad trapeziform projection represents the median eyeplate and the slender processes which flank it on each side are flaps of tissue which partially cover the depressions on the dorsal surface of the proximal region of the antennules.*

The function of these peculiar antennular organs is unknown. At one time it was thought that they were some form of statocyst but it is difficult to see how they could so function. The depression is very shallow and the flap of tissue which arises proximally to it does not close down over it to form any kind of a lid but stands up more or less vertically behind it. In all the species I have seen it is too small to form a complete cover for the pit. No statoliths or any foreign bodies have ever been recorded as being present in the pits but in *H. falklandica* there are, at the base of each pit, two or three small rounded darker areas which stain more readily than the surrounding tissues, but they are not detachable.

*Since this paper went to press I have received a letter from Mrs Tchindonova saying that, on further examination, they fully accept my suggested interpretation of the eyeplate and the lateral flaps of tissue. They add that careful examination revealed two lateral groups of colourless granules on the median eyeplate.

It seems obvious that these organs have some kind of sensory function. There is no evidence that they are auditory organs, but, since the animals have no functional eyes, it may well be that they serve as receptors of stimuli enabling individuals of the same species to find one another. I have (1955) suggested that they may be chemoreceptors but this is only conjectural.

For purposes of comparison I give herewith a figure of the anterior end in dorsal view of an adult female of *H. fyllae* taken off the west of Ireland. This shows the anterior margin of the carapace, the proximal portions of the antennules and antennae and the fleshy triangular median pad which I consider to be the eyeplate (Fig. 2). The homology of the structures shown is fully discussed below.

HANSENOMYSIS ANTARCTICA Holt and Tattersall

(Fig. 1.)

Hansenomysis antarctica Holt and Tattersall, 1906, b, p. 6.
Hansenomysis antarctica, Tattersall, 1908, p. 23, figs.
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Occurrence

Station GLD-4. Ross Sea, 76° 31′S. 164° 55′E., 27.11.58, 06.15–07.00 hrs., 4′ Blake Trawl, 587.1 m., 1 immature female, 17 mm.

Station GLD–16. Off Coulman Island, 73° 46.7′S. 169° 09′E., 2.12.58 01.30–02.15 hrs. 731 m., triangular dredge. One adult female in bad condition with posterior end of telson missing. Estimated length 25 mm. ; pleon and tail fan of female with telson intact.

Descriptive notes

The telson is complete in the immature specimen from the Ross Sea and in the fragment captured off Coulman Island which appears to have come from a more mature animal. Both of the whole specimens are in moderately good condition and it is therefore possible to clarify certain points which, owing to the poor material available in the past, have remained in some doubt.

Carapace. The antero-lateral angles of the carapace are bluntly rounded. Hansen (1913, p. 8), when recording a male from Graham Region, noted that in it these angles were less pronounced than in Tattersall's figure (1908, Pl. V, figs. 1–2) and suggested that this might be a sexual difference. In the present females the antero-lateral angles are more produced than in Hansen's figure (1913, Pl. I, fig. 2) but are smaller than in Tattersall's figure. The appearance of the contour of the anterior margin of the carapace varies considerably with the angle from which it is viewed. The whole of the anterior region of the carapace is quite strongly convex and if it is flattened by the weight of a cover-slip the antero-lateral angles appear to be much less produced than in an uncovered specimen as a result of the greater foreshortening of the more convex median region in the latter. It is possible that some of the differences in this character may be explained in this way but the question can only be answered when further specimens of both sexes are available for study.

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Eyes. In all the known species of *Hansenomysis* the eyes are reduced and lack all visual elements. In *H. antarctica*, *H. falklandica* and the new species, *H. angusticauda* which is described below, the eyes are represented by a small median eyeplate from which two triangular, bluntly-rounded, somewhat divergent lappets project forward. I have suggested above that in *H. fyllae* and, probably in *H. armata* also, the eyes are represented by a single median eyeplate which, however, is not produced forward into triangular divergent lappets.

Fig. 1—*Hansenomysis antarctica* H & T. Telson and uropods. ×15.

Telson. It is evident that the distal end of the telson as reconstructed by Tattersall is too short and too truncate. From Fig. I it will be seen that its broadest part is at about two thirds of its length from the base and that the telson extends for one fifth of its length beyond the apex of the exopod of the uropod. The spines arming the lateral margins are more definitely arranged in series than Tattersall surmised, with the long spines very long and slender and the smaller spines between them relatively very much smaller. (Fig. 1).

Uropods. Exopod as described for the type. Endopods, which were both broken off in the type, about half as broad as the exopods and subequal in length to them (Fig. 1).

Distribution

The species probably has a circumpolar distribution in the Antarctic. It has been recorded from off Coulman Island in the Ross Sea at 100 m.; from Graham Region at 385 m. and from the northern region of the Bellingshausen Sea in depths of 100–385 m. One specimen and the fragment in the present material were taken off Coulman Island and one female farther south off Terra Nova Bay.

HANSENOMYSIS ANGUSTICAUDA n. sp.

(Figs. 3–10.)

Hansenomysis antarctica, O. S. Tattersall, 1955. p. 59, figs.

Occurrence

Station GLD–9. Ross Sea, 75° 15′S. 165° 55′E. 29.11.58, 15.00–15.45 hrs. 808·4 m., 28 dia. Ring net. Vertical haul from bottom to surface. One imm. female, with oostegites just beginning to show, 26 mm. Holotype female U.S. Nat. Mus. Cat. No. 106973; allotype male, Brit. Mus. Nat. Hist. Reg. No. 1958. 11. 19. 203.

Description

Integument very soft and flexible. *Carapace* extremely short, leaving the posterior three thoracic somites completely exposed in dorsal view; anterior end not produced but evenly convex with the rim slightly upturned; antero-lateral angles produced into acutely pointed spine-like angles (Figs. 6, 10) which project very slightly beyond the anterior margin of the carapace. In the median line anterior to the cervical sulcus there are two small acute spines and a third is borne immediately posterior to the sulcus. The hepatic spines are short, very strong proximally and acutely pointed. Posterior to the sulcus the carapace on each flank is thickened and raised into two longitudinal keels. The central region between these keels forms an oval depressed area which appears to mark the region of the attachment of the carapace to the thoracic somites. The anterior inner angle of the thickened keel projects and appears as a definite spine in lateral view. From this the line of thickening of the carapace runs obliquely backward down the side of the carapace on each side. A small, very sharp spine is borne at about the middle of the anterior border of the lateral area of thickening and, from it, a smaller keel runs backward parallel to the ventral margin of the carapace. Half way along the border of the depressed central area on each side a small spine-like process marks the anterior end of a smaller keel which runs backward parallel with the lateral keels. Finally, there is at the middle point of the posterior end of the oval area a well marked forwardly-projecting spinous process from which a median keel runs back almost to the posterior margin of the carapace. (Figs. 6, 9, 10).

The anterior margin of the tergum of both the seventh and eight thoracic somites is produced forward dorsally to overlap the preceding somite. In the sixth somite the tergum is produced on its dorsal anterior margin to form a thin semicircular flap which extends forward and upward beyond the middle of the fifth thoracic somite (Fig. 10).

Abdomen slender and sinuous in lateral view : first somite with the tergum thickened and produced both anteriorly and posteriorly to cover the adjacent somites to produce the saddle-like appearance which has been described also in *H. antarctica, falklandica* and *armata*. (Fig. 10).

Second to the fifth abdominal somites sub-equal in length ; sixth more than twice as long as the fifth.

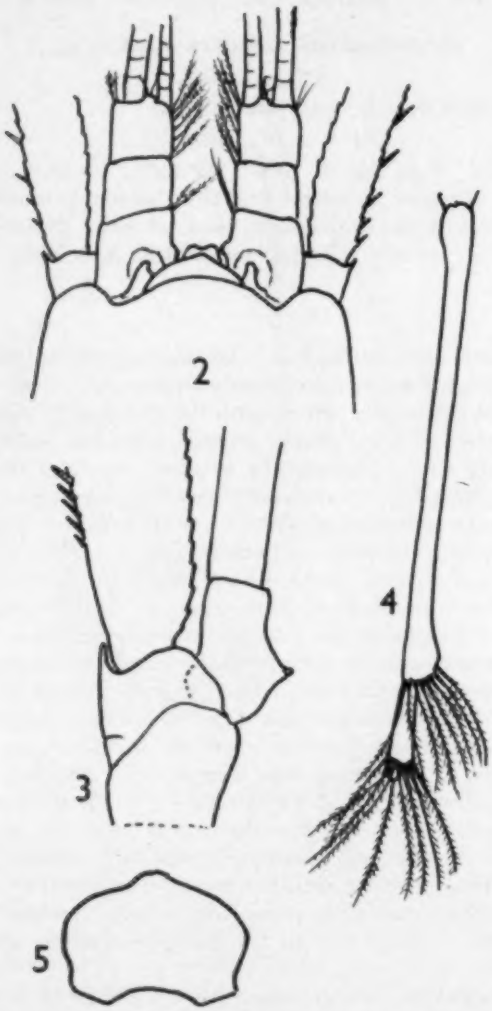
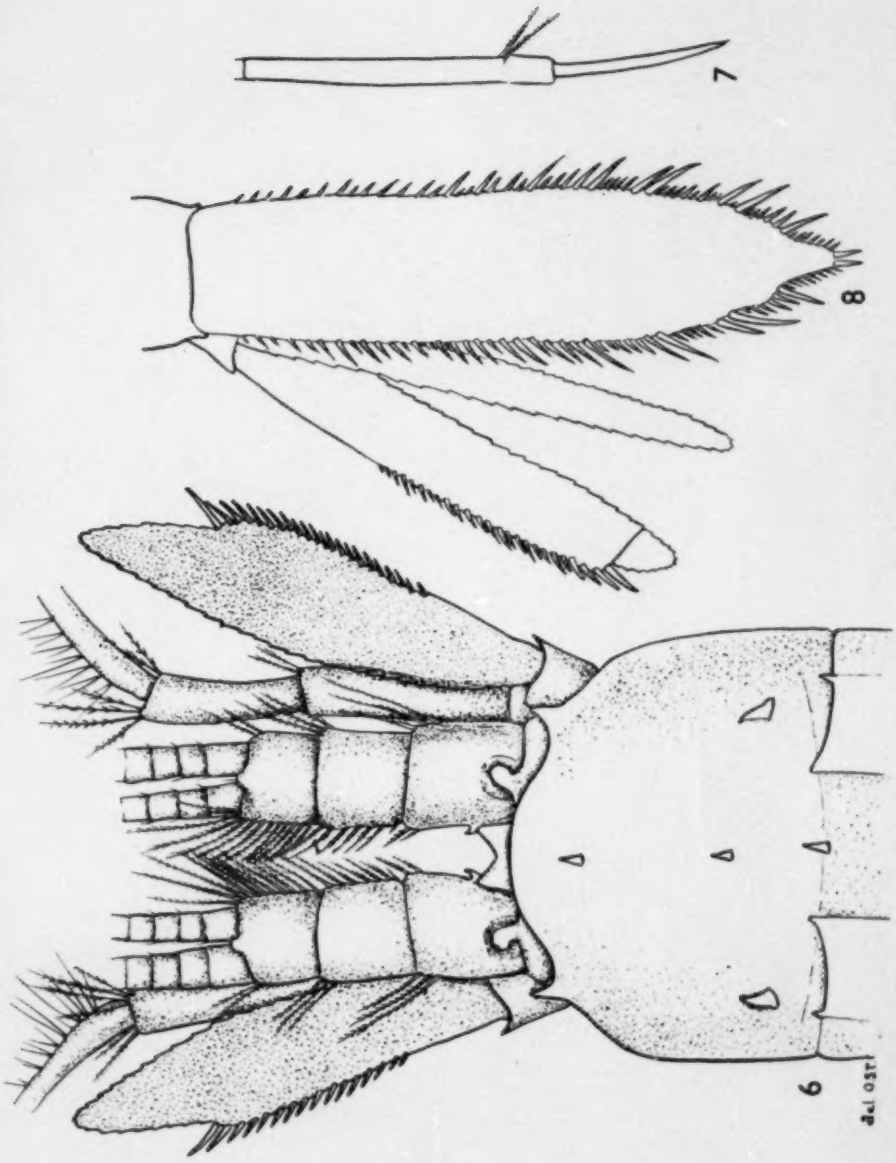
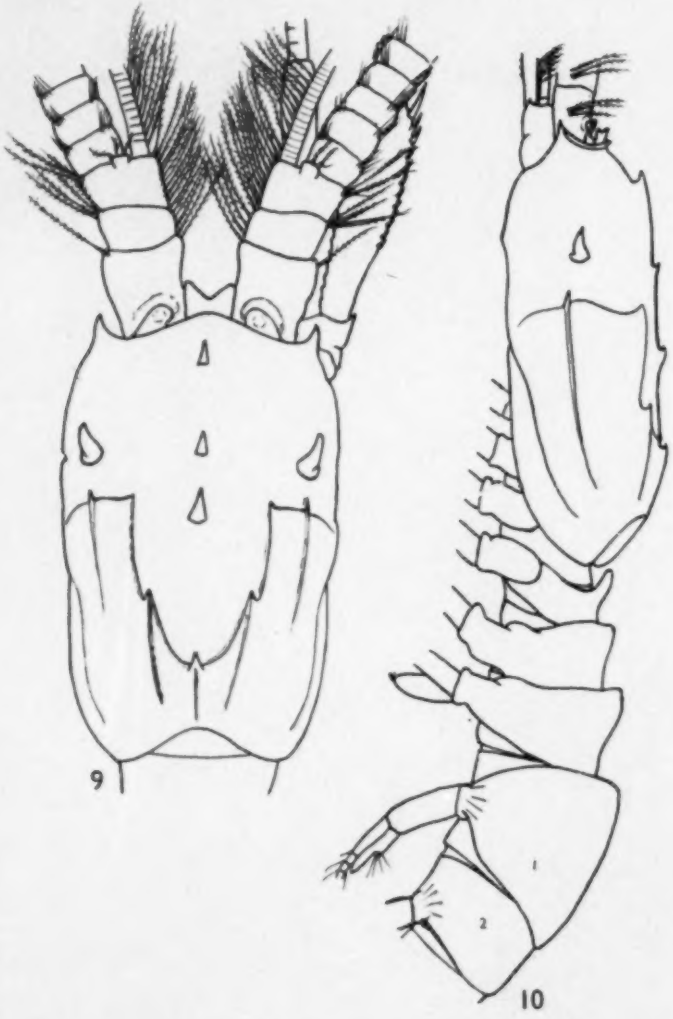


Fig. 2—*Hansenomysis fyllae* (Hansen). Anterior end of adult female in dorsal view.
Figs. 3–5—*Hansenomysis angusticauda* sp. n.
3—Proximal portion of antenna. 4—Fifth pleopod of immature female. 5—Labrum in ventral view.



Figs. 6–8—*Hansenomysis angusticauda* sp. n.
6—Anterior end of immature female in dorsal view. ×15. 7—Distal end of fourth thoracic endopod. ×18. 8—Telson and left uropod of immature female. × 15.

Antennular peduncle short and robust ; inner margins of second and third segments armed with a closely set row of long plumose setae which are relatively longer in the male than in the female ; well developed pit-like depression present on the dorsal surface of the proximal end of the first segment ; a rounded flap of thin tissue arising from the arthrodial membrane immediately proximal to the pit projects upward and forward, partially covering the depression.



Figs. 9–10—*Hansenomysis angusticauda* sp. n. (after O. S. Tattersall 1955 as *H. antartica*).
9—Anterior end in lateral view of adult male. × 15. 10—Anterior end in dorsal view of adult male. × 15.

On the inner margin of the segment, about one third of its length from the base, there is a short, acutely pointed, forwardly curving process looking like a strong hook. In other species of the genus a small protuberance appears in this position (Fig. 6).

Antenna. *Sympod* relatively slender, with the outer distal angle produced into a long acute spine. *Peduncle* relatively long and slender, extending beyond the antennular peduncle by more than half the length of the third segment ; first segment rather long, with a large conical projection on the proximal half of its inner ventral margin. The apex of this protuberance is transparent and shows up markedly under the microscope as a clear bright spot looking like the aperture of a pore. In one specimen there is an amorphous mass attached to it which might possibly be the remains of some exudation from it. (Fig. 3).

Scale oval, nearly five times as long as its greatest breadth ; extending for nearly a fourth of its length beyond the distal margin of the antennular peduncle ; proximal fourth of outer margin naked ; thence armed with a close row of 17–22 evenly graduated spines which increase in size distally and occupy about half of the margin ; distal fourth of margin setose, the setae extending around the narrow apex and along the whole of the inner margin (Fig. 6).

Eyeplate in the form of a large, narrow fleshy plate projecting forward in the median line from beneath the convex anterior margin of the carapace to the level of the anterior rim of the pit-like depression on the antennular peduncles but not in any way covering them laterally ; produced distally into triangular lappets which have their outer margins straight and almost parallel but their inner margins converging to meet in the median line at an angle of about 50°. There are no traces of any visual elements on the eyeplate (Fig. 6).

Mouth parts. As far as can be seen without dissection there is nothing very different in the form of the mouth parts from those in other species of the genus. The *labrum* is large and broad, with the anterior margin only slightly produced in the median line to form a very short rounded apex ; posterior margin concave (Fig. 5).

Thoracic appendages. First and second pairs of the same shape as in the published description for the genus. *Endopods of the third to the fifth pairs* long and slender, terminating, as in other members of the genus, in a minute chela formed by the dactylus with two strong spines and densely covered with small setæ. *Sixth to the eighth thoracic endopods* very long and slender with the carpus longer than the propodus and the small dactylus bearing a very long and slender nail (Fig. 7).

Pleopods of the female of the usual type found in the genus ; fifth pair very long, extending almost to half the length of the telson when stretched backward. As the specimen is by no means adult it is possible that in larger females the pleopods may be relatively even longer (Fig. 4). When referring the badly damaged male specimen captured by the " Discovery " to *H. antarctica* (1955, p. 60) I recorded that the pleopods were of the same form as those found in *H. fyllae* but that the endopod of the fifth pair was considerably longer than the exopod

and that the first pair appeared to differ from other species of the genus in having a two-segmented endopod. The articulation, however, was obscure and may not have been complete.

Uropods long and slender ; exopod and endopod sub-equal in length ; proximal segment of exopod ten times as long as the distal ; outer margin unarmed for the proximal two fifths of its length ; distal three fifths armed with a close row of twenty-one to twenty-three graduated spines, increasing in size distally. There is a slight tendency towards an arrangement of the spines into a series of larger spines with smaller ones in the spaces between them ; endopod much more slender than the exopod. (Fig. 8).

Telson long and narrow, with lateral margins almost parallel for three fourths of their length and then converging evenly almost to the apex ; near the apex the margins are concave and thence nearly parallel to the narrowly rounded apex itself ; armed with a very close row of spines arranged in a series of from six to eight very long slender spines with four to six graduated spines in the spaces between them in the distal half of the series. Proximally the series becomes more irregular with less difference between the larger and smaller spines. The apical region armed distally with two long spines and laterally with eight small even ones on each side (Fig. 8).

Length of immature female 26 mm.

Remarks

This species can be distinguished from *H. antarctica*, which in many respects it closely resembles, by the relatively longer and more slender antennal scale bearing 17–23 spines on its outer margin compared with 11–15 spines in *antarctica* ; by the sculpturing of the carapace with its antero-lateral angles produced into spine-like processes, whereas in *antarctica* these are evenly rounded and not greatly produced ; by the longer, more slender uropods with a greater number of more crowded spines arming the exopods and, above all, by the longer and much narrower telson with the lateral margins parallel and less convex than in *antarctica*.

It would appear that *angusticauda* is a larger form than *antarctica* for the immature female of the latter in this collection measures 17 mm. and its oostegites are all showing clearly. W. M. Tattersall gave the length of his type—an ovigerous female—as 20 mm. It is true that in this specimen the distal end of the telson was missing, but from the length of the exopod of the uropod in his figure and in the light of the undamaged specimens of *antarctica* in the present collection, I do not think that his adult female could have measured more than 22–23 mm. The undamaged specimen of *angusticauda* is an immature female measuring 26 mm. and its oostegites are only just beginning to show.

The form of the antennal peduncle and of the sympod in the present specimen of *angusticauda* differs somewhat from the figure of the antenna which I gave for the " Discovery II " specimen in 1955. Thanks to the great kindness of Dr I. Gordon of the British Museum, I have been enabled to re-examine the " Discovery I " specimen. In dorsal view it appears just as in the published

figure (the drawing was made *in situ* and the specimen is old and somewhat brittle so that it will not bear much manipulation) and there is a protuberance on the dorsal region of the proximal end of the first segment of the peduncle. This projects beyond the outer lateral margin and looks like a blunt spine. In dorsal view the very marked conical protuberance from the inner margin of this segment is invisible since it lies somewhat ventrally and projects downward very much in the vertical plane.

I give herewith a key for the identification of the species of this most remarkable genus. The form of the telson in *armata* is unknown since it had been broken off in the type specimen, but the species can readily be distinguished by the shape of the eyeplate and by the armature of the antennal scale and the exopod of the uropod.

KEY TO THE DETERMINATION OF THE SPECIES OF THE GENUS *HANSENOMYSIS*

Antennal scale setose all round with spines among the setae on the outer margin	1.
Antennal scale armed with spines and no setae on proximal part of outer margin ; small distal portion of margin setose. Eyeplate produced anteriorly into two lappets	3.
1. Outer margin of first segment of exopod of uropod setose with some spines among the setae	2.
Outer margin of first segment of exopod of uropod armed with spines and no setae. Eyeplate trapeziform	*H. armata* Birstein & Tchindonova
2. Telson one and a half times as long as uropods ; proximal fifth of lateral margins unarmed ; 9–10 spines among setae of outer margin both in the antennal scale and the exopod of uropod. Eyeplate produced into lappets	*H. falklandica* O. S. Tattersall
Telson only slightly longer than uropods ; proximal three fifths of lateral margins unarmed. 5–6 spines among setae both in the antennal scale and exopod of uropod. Eyeplate triangular	*H. fyllae* (Hansen)
3. Carapace sculptured into keels and armed with spines ; antero-lateral angles of carapace produced into acute processes. Telson long and narrow ; proximal three fourths of lateral margins parallel.	*H. angusticauda* n. sp.
Carapace bearing obscure keels with only two pairs of spines ; antero-lateral angles rounded. Telson relatively broad with lateral margins slightly convex ; proximal fifth of lateral margins unarmed	*H. antarctica* Holt & Tattersall

Sub-family **Mysinae**

Tribe Erythropini

Genus *PSEUDOMMA* G. O. Sars, 1870

Pseudomma G. O. Sars, 1870, p. 154.
Pseudomma G. O. Sars, 1870–9, vol. 1, p. 47.
Pseudomma, Illig, 1930, p. 571.
Pseudomma, O. S. Tattersall, 1955, p. 91.

PSEUDOMMA BELGICAE (Hansen in MS), Holt and Tattersall

Pseudomma belgicae Holt and Tattersall, 1906 *b*, p. 8.
Pseudomma belgicae, Hansen, 1908, p. 12, figs.
Pseudomma belgicae, Tattersall, 1908, p. 27, figs.
Pseudomma belgicae, Hansen, 1913, p. 11, figs.
Pseudomma belgicae, O. S. Tattersall, 1955, p. 94.

Occurrence

Station GLD–9. Ross Sea, 75° 15′S. 165° 55′E., 29.11.58, 15·00–15·45 hrs., 808·4 m., 28″ dia. Ring net ; vertical haul from bottom to surface, 1 adult female with empty brood sac, 23 mm.

Station GLD–14. Ross Sea, 74° 25·1′S. 167°E., 1.12.58, 04.00–09.45 hrs., 731·6 m., Alaska fish trap dragged along bottom with drift of ship. One adult female, 23 mm.

Distribution

This species has a circumpolar distribution within Antarctic waters. The types were taken in the Ross Sea not far from the localities in which the present specimens were taken.

PSEUDOMMA ARMATUM Ransen, 1913

Pseudomma armatum Hansen, 1913, p. 12, figs.
Pseudomma armatum, Rustad, 1930, p. 7.
Pseudomma armatum, O. S. Tattersall, 1955, p. 92.

Occurrence

Station GLD–8. Ross Sea, off Terra Nova Bay, 75° 30′S, 165°44′ E., 29.11.58, 09.45–10.45 hrs., 631 m., 4′ Blake Trawl, 1 adult female with empty brood sac—distal end of telson and uropods missing, estimated length 30 mm.

Remarks

The present specimen is so badly damaged that it is not possible to be completely certain of its identity. The proportions of the antennal scale and the form of the ocular plate with two well marked projections on its anterior margin, one on either side of a distinct median notch are very similar to those found in *P. armatum*. The telson is broken off but from the portion which is left it is clear that the spines arming the lateral margins extend much nearer to the base than in the published descriptions of the type—leaving a much shorter portion of the margin unarmed.

A second point of difference is that of size. The adult type, which was captured off South Georgia, measured 17 mm. O. S. Tattersall (1955, p. 62) recorded adults of up to 22·4 mm. from around South Georgia and stated that animals of 16–17 mm. were obviously immature. The present specimen has lost the distal ends of both telson and uropods but from the length from the anterior margin of the carapace to the anterior margin of the telson it is clear that it must have measured about 30 mm. It was, however, captured in the Ross Sea nearly 20° farther south, than any previous records. This might account for its greater size. A third point which gives rise to some doubt as

to its identity is the locality at which the present specimen was taken—so very distant from all previous records.

Distribution

Previously known only from around South Georgia and South Orkneys.

Tribe Leptomysini

Genus *MYSIDETES* Holt and Tattersall, 1906

Mysidopsis G. O. Sars, 1885?, p. 202.
Mysideis (pars) Holt and Tattersall, 1905, p. 127.
Mysidetes Holt and Tattersall 1906 *a*, p. 39 ; *b*, p. 10.
Metamysidella Illig, 1906, p. 210.
Mysidetes, Tattersall, 1908, p. 32.
Mysidetes, O. S. Tattersall, 1955, p. 141.

MYSIDETES POSTHON Holt and Tattersall

Mysidetes posthon Holt and Tattersall, 1906 *b*, p. 10.
Mysidetes posthon, Tattersall, 1908, p. 33, figs.
Mysidetes posthon, Hansen, 1913, p. 17, figs.
Mysidetes posthon, Tattersall, 1923 p. 287.
Mysidetes posthon, O. S. Tattersall, 1955, p. 142.

Occurrence

Station D. Stomach of *Trematomus barnacchii* Boulenger captured in McMurdo Sound off Hut Point. 23.12.58, 1 male, 19·5 mm. in very bad condition.

Station EAD–2. McMurdo Sound off Inaccessible Island, 77° 39·4′S. 166° 39·4′S., 19.2.60, 19.45–20.40 hrs., 315 m., 4′ Blake Trawl, 1 imm. male 1 imm. female, both 17 mm, in very bad condition.

Remarks

All three specimens which, with some reserve, I here refer to *M. posthon*, are in very poor condition but, except for comparatively minor differences, they do agree closely with the published descriptions and figures of this species. In the past, workers have drawn attention to the considerable individual variation which occurs in specimens which they have examined and have referred to *M. posthon*. I think that the slight variations which are present in the specimens in this collection are not of sufficient importance to warrant their exclusion from the species.

Distribution

The types of *M. posthon* were taken in the Ross Sea near the " Discovery " Winter Quarters and another record is from off Coulman Island. The species has since been collected by all the principal Antarctic Expeditions. It has been recorded from the Ross Sea, the Bay of Whales, Scotia Sea, off the South Shetlands, the South Sandwich Islands, South Georgia and the Palmer Archipelago. The present record from far south in the Ross Sea is the most

southerly latitude in which it has been taken. The most northerly record is from near Kerguelen Island (about 49°S.) so the species has a very considerable range of latitude.

Tribe Mysini

Genus *ANTARCTOMYSIS* Coutière

Mysis Holt and Tattersall, 1906 *b*, p. 11.
Antarctomysis Coutière 1906, p. 1.

Remarks

This genus was originally founded for forms which resembled the genus *Mysis* in the form of the antennal scale and the telson and uropods, but differed in the form of the male pleopods. In *Mysis* the first, second and fifth pairs are reduced as in the female although, in some cases, the fifth pair may be two-segmented. The third pair is biramous with a simple, short unsegmented endopod bearing a long well developed psudobranchial lobe at its base and a short 4–6 segmented exopod. The sympod of the fourth pair is long and two-segmented ; the endopod is similar to that of the third pair though it may be two-segmented but the exopod is greatly elongated, composed of 6–7 segments ; the penultimate and the very short ultimate segments each bearing a single very long strong seta. These setae together form a pincer-like termination to the exopod.

In *Antarctomysis* only the first and second pairs are reduced as in the female. The third pair are biramous, small and unmodified with both rami many-segmented and normal. The fourth pair are biramous and similar in form to those of the third pair ; the exopods are elongated and composed of about fifteen segments ; ultimate segment armed with two long setae, the penultimate segment with one extremely long seta. The sympod is two-segmented. The fifth pair also are biramous with both rami multi-articulate and unmodified but the exopod is slightly longer than the endopod. The sympod is two-segmented.

Thus it is not difficult to identify male specimens of *Antarctomysis* but it is by no means easy to identify females. Holmquist (1959, p. 30) gave a number of characters whereby females and juveniles of this genus may be distinguished from those of species of the genus *Mysis*. I think that I have found a further character which I have not seen mentioned in the literature. I find that in both the known species which are at present included in the genus *Antarctomysis* all the males and immature females have well developed sternal processes on the third to the seventh thoracic somites. There is a blunt protuberance on the sternum of the second somite and in *Antarctomysis ohlinii* there is a short, straight, acutely pointed process on the eighth somite between the strong genital organs of the males. In *A. maxima* this last process does not appear to be so well developed as in *ohlinii* but can be seen as a small boss even in large males. In adult females there is no trace of sternal processes on the fifth to the eighth somites but very small, acutely pointed processes do occur on the third and fourth somites.

A very small tubercle can be seen on the second thoracic sternum in juveniles of *A. ohlinii* but I have been unable to find this in *maxima*.

The processes which occur in the males and young females are long and delicate, arising from the median line of the sternum at about the middle of its length. They are usually curved forward but in some cases they may be straight and at right angles to the ventral surface of the somite. They are very difficult to see without complete removal of the thoracic appendages.

The two species which are included in the genus *Antarctomysis* are found in the same localities and are often taken in the same haul. At first sight it is not easy to distinguish them and the best guides to their identification are the form of the eyes and the armature of the sympod of the antenna. In *maxima* the eyes are large and short with the cornea extending over the whole of the distal end and outer region of the organ, so that the eyes look essentially outward and forward. In *ohlinii* the eyes are not so broad but are longer and more cylindrical in shape and the cornea occupies only the distal region of the organs so that they look essentially forward.

In *A. maxima* the sympod of the antenna bears on its ventral surface two acute spines situated one at the inner distal angle and one at the outer. In *A. ohlinii* only the outer distal angle bears a spine, the inner distal angle being evenly rounded.

ANTARCTOMYSIS MAXIMA (Hansen in MS) (Holt and Tattersall)

Mysis maxima (Hansen in MS) (Holt and Tattersall), 1906 *b*, p. 11.
Antarctomysis maxima, Coutière, 1908, pp. 1–7, figs.
Antarctomysis maxima, Hansen, 1908, p. 13, figs.
Antarctomysis maxima Tattersall, 1908, p. 36, fig. ; 1913, p. 872 ; 1918, p. 12 ; 1923, p. 301.
Antarctomysis maxima, Hansen, 1913, p. 19.
Antarctomysis maxima, Zimmer, 1915, p. 203, figs.
Antarctomysis maxima, Hardy and Gunther, 1935, p. 201, fig.
Antarctomysis maxima, O. S. Tattersall, 1955, p. 171.

Occurrence

Station M. McMurdo Sound, Ross Island, Winter Quarters Bay. Hole blasted in ice and kept open by hand. Depth of water 37·5 m.

6.5.59. No gear specified, 1 adult male, 48 mm.
8.5.59. Bottom trawl, 1 adult male, 45 mm.
13.5.59. Bottom trawl, 1 adult male, 46 mm.
25.5.59. Bottom trawl, 1 adult male, 46 mm.

Station EAD–2. McMurdo Sound, off Inaccessible Island, 77° 39·4′S, 166°16′E., 19.2.60, 19.45–20.40 hrs. 315 m. 4′ Blake Trawl. One immature female with oostegites only just beginning to show, 30 mm., 1 posterior end of immature female of *Antarctomysis* species.

Remarks

The capture of this species in a depth of 37·5 m. is most unusual. It has rarely been recorded from less than 50 m. and is usually found in much deeper water.

Distribution

A. maxima is one of the commonest species in the Antarctic and the colder regions of the southern Atlantic, occurring in large numbers in the Ross Sea,

Weddel Sea, off Graham Land, off the Falkland Islands, the South Orkneys, South Georgis and South Sandwich Islands.

ANTARCTOMYSIS OHLINII Hansen

Antarctomysis sp. Tattersall, 1908, p. 36, figs.
Antarctomysis ohlinii Hansen, 1908, p. 13 ; 1913, p. 20, figs.
Antarctomysis ohlinii, Tattersall, 1923, p. 300.
Antarctomysis ohlinii, Rustad, 1930, p. 21.
Antarctomysis ohlinii, O. S. Tattersall, 1955, p. 177.

Occurrence

Station GLD–5. Ross Sea, 76° 11·6′S. 164° 46′E., 27.11.58, 14·00–15·00 hrs., 695 m., Triangular dredge. One imm. female 22 mm.

Station GLD–9. Ross Sea, 75° 15′S. 165° 55′E., 29.11.58, 15.00–15.45 hrs., 808·4 m., 28″ dia. Ring net. Vertical haul, bottom to surface. Two imm. females 23 mm.

Station GLD–10. Ross Sea, 75° 06′S. 165° 52′E., 29.11.58, 15.45–17.00 hrs., 832·2 m., 4′ Blake trawl. One adult female with empty brood sac, 54 mm.

Station GLD–14. Ross Sea, 74° 25·1′S. 167° 00·3′E., 1.12.58, 04.00–09.45 hrs., 731·6 m., Alaska type fish trap which dragged on the bottom as the ship drifted. Two adult males (one in two pieces) 54 and 55 mm.

Station G. McMurdo Sound, off tip of Cape Armitage. Ice crack opened by hand. From stomach of Weddel seal taken in 4·4–5·5 m.

2.2.59. One immature male, 35·5 mm.

6.2.59. One adult male, 52 mm. ; 1 ovigerous female 54 mm.

Station EAD–2. McMurdo Sound off Inaccessible Island, 77° 39·4′S. 166° 16′E. to 77° 40·8′S. 166° 16·5′E., 19.2.60, 19·45–20·40 hrs., 4′ Blake trawl. 1 imm. female 30 mm. Badly damaged.

Distribution

This species has the same distribution as the last species, *Antarctomysis maxima* and has frequently been taken with it.

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VARIABILITY IN THE BEHAVIOUR OF WILD HOUSE MICE (*MUS MUSCULUS* L.) TOWARDS LIVE TRAPS

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Groups of marked wild house mice confined in pens were subjected to repeated live-trapping, to investigate suspected differences in reaction to traps. More males tended to enter traps than females, but the difference between the sexes was not consistently statistically significant. Within each sex, however, some individuals were significantly trap-prone, and some trap-shy. This heterogeneity in response was more pronounced among the females, and there was evidence that it was due to social factors involving the presence of males. The trap-response of descendents of trap-prone and trap-shy mice suggested that inherent differences might also be involved.

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INTRODUCTION

In 1953 one of us was collecting wild house mice by live-trapping a heavy infestation in a grain store, and saw differences in the reactions of individuals when they first encountered traps. It was clear that captures were determined not only by the numbers and siting of the traps but also by variation in the investigatory behaviour of the mice. This observation recalled the work of Young *et al.* (1952) who found that the frequencies of recapture of marked free-living house mice showed large deviations from those expected if the animals were recaptured in a randum manner.

It was decided to confine a number of the trapped mice in a large pen and subject them to repeated live-trapping, for under controlled conditions,

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corroboration of the findings of Young and his co-workers might also throw light on the factors responsible. The preliminary results led at once to the study of further confined populations, but statistical analysis of the data has only recently been undertaken, for comparison with the findings of Andrzejewski *et al.* (1959), who have carried out a similar investigation.

MATERIAL AND METHODS

The colonies were confined in circular pens approximately six metres in diameter and furnished with fourteen large wooden nest boxes. Hay was periodically scattered about to provide nesting material, and water, wheat and oats were constantly supplied in excess at numerous feeding stations. The mice were individually marked by toe-clipping, some weeks before trapping commenced.

Longworth traps were used exclusively (see Chitty & Kempson 1949) and the food in the traps was identical with that in the pen. Trappings were carried out for one night only at intervals of fourteen days, the traps being set at 18.00 hrs and the occupied traps removed every three hours until 06.00 hrs the next morning. Thus the trap-night was divisible into four equal three-hourly periods, and the catch period was separately recorded. After the last catch had been removed, the uncaught mice were checked by surrounding the nest boxes with portable sheet-metal barriers, and catching the mice by hand. The animals in the traps were then identified and released into the pen. The colony remained free from outside interference until the next trapping.

RESULTS

1. *Mice obtained by live-trapping.*

The experiment began with twenty-four males and twenty females. A number of deaths occurred before the final trapping, but these have been taken into account in the calculations. On every occasion a proportion of the animals

Table 1—Numbers of mice caught during seven trap-nights at intervals of 14 days.

Trapping	No.of traps	Number of mice caught					Not caught	Total at risk
		18.00–	21.00–	24.00–	03.00–	TOTAL		
1	60	7	10	5	3	25	19	44
2	78	17	7	2	5	31	12	43
3	80	14	4	6	3	27	15	42
4	80	12	8	6	5	31	10	41
5	80	16	6	3	4	29	11	40
6	100	21	5	2	5	33	6	39
7	80	11	5	2	5	23	13	36

failed to enter traps, although excess traps were supplied. Even when the number of traps was increased to more than twice the number of mice (sixth trapping) one quarter of them were not caught (Table 1).

A constant probability of capture per mouse throughout the entire trapping period showed that the behaviour of the mice towards the traps underwent no general change, and if it is assumed that the probability of a mouse being caught remained constant throughout a trap-night, the numbers caught in successive periods throughout the night also showed no significant variations from the numbers expected. In addition, there were no significant differences in the proportions of males and females caught in the seven trappings, and hence no evidence of greater susceptibility of males to trapping (Table 2).

When the composition of the samples is taken into account, however, there is evidence in both sexes of individual differences in behaviour towards traps. If the probability of catching each individual were the same, the frequencies of the numbers of captures per mouse would be expected to follow the binomial distribution. But the number of mice which entered the traps on all seven trap-nights clearly exceeds expectation (Table 3), as does the number caught only once or twice, or not at all. The chi-square testing deviation from the expected binomial distribution is 64·02 (18 d.f. $P=<\cdot001$) for the males, and 50·61 (16 d.f. $P=<\cdot001$) for the females. Thus, although excess traps were available, there was not the same probability of capture for each individual ; in both sexes there were some animals particularly likely to be caught (trap-prone) and others unlikely to be caught (trap-shy).

Further to this, analysis of the records of the times of capture during each trap-night shows that the time of capture is not independent of the likelihood of being captured (Table 4). The chi-square of heterogeneity for the males is 23·79 (6 d.f. $P=<\cdot001$) and for the females 19·69 (6 d.f. $P=<\cdot01$). Inspection of Table 4 shows that the heterogeneity is mainly due to the high probability that a trap-prone mouse will enter a trap within the first few hours

Table 2—Numbers of males and females caught in each trapping.

Trapping	Number of traps	Caught		Not caught		Heterogeneity chi-square
		Male	Female	Male	Female	
1	60	14	11	10	9	0·05
2	78	16	15	8	4	0·79
3	80	15	12	9	6	0·08
4	80	15	15	8	3	1·69
5	80	18	11	5	6	0·91
6	100	19	12	3	5	1·46
7	80	12	9	7	8	0·39

of its being placed in the pen. Less pronounced, but also clear, is the tendency for trap-shy individuals to enter later.

As the experimental animals were obtained by live-trapping and hence may have been selected for trap-proneness, the results suggested that free-living populations might contain a higher proportion of trap-shy animals than that detected. It seemed desirable to repeat the experiment with mice never previously subjected to trapping. In this respect the apparent absence of any difference between the sexes in behaviour towards traps also required further investigation, for trapped samples of rodents commonly show a discrepancy of females due to the greater activity of the males. The result could be a consequence of using a sample containing females selected for trap-proneness or

Table 3—Frequency distribution of numbers of captures.

Number of times caught	MALES		FEMALES	
	Numbers of mice	Expected numbers	Numbers of mice	Expected numbers
0	1	0·00	0	0·02
1	1	0·09	2	0·16
2	2	0·73	2	0·77
3	1	2·27	2	2·34
4	4	4·75	2	4·49
5	1	5·89	1	5·10
6	2	4·12	3	3·24
7	7	1·27	5	0·88

Table 4—Frequency of capture according to interval of trap-night.

	Interval	Number of times caught						
		1	2	3	4	5	6	7
Males	18.00–	–	–	–	6	2	3	35
	21.00–	–	2	–	6	–	3	8
	24.00–	–	–	1	2	2	2	4
	03.00–06.00	1	2	2	2	1	4	2
Females	18.00	–	1	2	1	1	12	24
	21.00–	2	–	1	1	3	4	6
	24.00–	–	1	2	3	–	1	3
	03.00–06.00	–	2	1	2	1	1	2

the provision of excess traps might have eliminated this discrepancy. Alternatively, it was also desirable, therefore, to test the effect of using far fewer traps than the number of animals at risk.

2. *Hand-caught males and females*

Two new colonies were established with house mice caught by hand during threshing operations. It was quite certain that these mice had never encountered live-traps. One colony (pen 2) was made up of 28 adults of each sex, and the other (pen 3) of 29 males and 27 females (due to an error in sexing one individual). After six weeks they were trapped on four occasions at fortnightly intervals. The trapping procedure for pen 2 was identical with that used for the original experiment, but for pen 3, only twenty-four traps were used and no attempt was made to distinguish early from late captures.

Within both pens there was no significant variation in the proportions of mice caught on the four occasions. A large proportion of the mice in pen 2 refrained from entering the traps at each trapping, for each time only about half of the traps were occupied. In pen 3, on the other hand, all of the traps were occupied on two occasions, and all but one on another, so the small number of traps clearly limited the numbers caught. Table 5 gives the numbers of males and females caught at each of the four trappings in the two pens, and the corrected heterogeneity chi-square indicating the significance of deviations from the numbers expected if the catches were proportional to the numbers at risk.

Table 5—Numbers of males and females caught at successive trappings.

Trapping	Pen 2 (66 traps)			Pen 3 (24 traps)		
	No. males caught	No. females caught	Heterogen. chi-square	No. males caught	No. females caught	Heterogen. chi-square
1	17	15	0·27	10	13	1·00
2	14	13	0·07	15	9	1·80
3	23	14	6·00*	17	7	5·68*
4	20	12	4·34*	16	4	8·66†

* significant at 5% level.
† significant at 1% level.

At the third and fourth trappings significantly greater proportions of males were caught in both pens. The data are, therefore, consistent with the hypothesis that males and females are initially equally likely to be caught, but with experience of traps, the trap-shyness of males tends to decrease, while that of females tends to remain the same, or increase. (The low numbers of females caught at the fourth trapping in pen 3 could not have been entirely due to pre-empting of the traps by males, for on that occasion four traps remained unoccupied).

The frequency of capture of the individual mice is summarized in Table 6. An unexpected result was that the frequency of capture of males in pen 2, with excess traps, showed no significant deviation from the expected binomial distribution (chi-square=34·47 with 27 d.f., P=>·05). The females, on the other hand confirmed the results of the first experiment, the number caught 0 or 1, and 3 or 4 times clearly exceeding expectation (chi-square=47·98 with 27 d.f., P=<·01). In pen 3 the numbers of males which either entered the traps on all occasions or avoided capture altogether, exceeded expectation (chi-square=46·0 with 28 d.f., P=<·05) and the number of females which avoided capture was also too high (chi-square=50·06 with 26 d.f., P=<·05).

Table 6—Frequency of captures among males and females with excess traps and insufficient traps.

No. times caught	Pen 2 (66 traps)				Pen 3 (24 traps)			
	Males		Females		Males		Females	
	Caught	Expected	Caught	Expected	Caught	Expected	Caught	Expected
0	0	0·4	3	2·0	3	1·80	10	6·28
1	5	2·9	12	7·5	9	7·25	8	11·04
2	6	8·5	1	10·5	7	10·88	4	7·28
3	11	10·9	8	6·5	5	7·25	3	2·12
4	2	5·3	4	1·5	5	1·80	2	0·23

Differences in the social status of the mice obviously had to be considered as a possible reason for differences in their trapping records. The social organization of these colonies was known ; a small number of males maintained individual territories from which all other mice, except one or more females, were driven whenever encountered, while the remaining males and females lived in large unstable groups. It seemed probable that these territorial males, being dominant and most active within areas which made up a considerable proportion of the pen, would appear to be trap-prone, especially when few traps were supplied. Similarly, the trapping record of a female might depend upon whether or not she was mated with one of the territorial males. The social status of the individuals in pen 2 was established (see Crowcroft 1955) and the trapping records re-examined in this light, but the figures were too small to supply conclusive evidence. Only seven of the 28 males were successful in maintaining territories. Of these three were caught once, two were caught three times, and two, four times. Six of these males had one mate and the seventh had two. Of these eight females, one missed capture, four were caught once and three were caught three times.

However, an alternative method of investigation was available. The females had showed the most marked and consistent division into trap-prone and trap-shy individuals in this social environment, but it was known that they took virtually no part in the aggressive behaviour which maintained it. Thus

the trap response of females in the absence of territorial behaviour could be examined simply by setting up a colony composed only of females.

3. *Females in the absence of males*

A new colony (pen 4) was set up containing 56 hand-caught adult females of the same stock as that used for pens 2 and 3 and never previously trapped. After a six weeks interval, this group was trapped four times with sixty traps at intervals of fourteen days. One female died before trapping began and another between the second and third trappings. There was very little aggressive behaviour ; although a few of the females made weak attempts to defend nest boxes against intruders, no territories were maintained. The mice lived in two large groups and all individuals wandered freely about the pen.

The frequency of capture of these females is given in Table 7. There is no significant deviation from the expected binomial distribution (chi-square=72·0 with 53 d.f., P=<·05) and no marked division into trap-prone and trap-shy individuals.

Table 7—Frequency of capture of female mice in the absence of males.

No. times caught	Number caught	Number expected
0	1	0·2
1	4	2·5
2	9	11·4
3	20	22·8
4	20	17·1

This result provided evidence that the variation in trap-response, at least of the females, was primarily due to social rather than inherent factors. But clearly, this evidence would be of greater value if it could now be shown that the presence of males changed the behaviour of these particular females into the pattern previously observed.

4. *Females in the presence of males*

The 54 females were divided into two equal groups by taking out a random sample of 27, stratified according to trapping record. Each group was combined with an equal number of fresh males of the same wild stock (pens 5 and 6). After a period of some weeks, during which the animals organised themselves in the manner described for pen 2, the trapping procedures adopted with pens 2 and 3 were repeated with pens 5 and 6 respectively.

In pen 5 (excess traps) there were, as before, no significant changes either in the proportion of mice caught at successive trappings or in the proportions of males and females in the catches. There was a tendency for more males to be caught, but this was significant only at one trapping. Analysis of the

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frequency distribution of the number of times each male was caught showed a significant deviation from the expected binomial distribution (chi-square 47·14 with 22 d.f., P=<·01) and a marked division into trap-prone and trap-shy individuals.

The females also showed a significant deviation (chi-square=38·79 with 22 d.f., P=<·05) and clearly a small number were either especially trap-prone or trap-shy. The females were classified according to their previous trapping records. Of the ten females which were caught on all possible occasions in pen 4, five were caught at all trappings in pen 5, but apart from this there appeared to be no marked association between the numbers of times each one was captured in the two series.

In pen 6 (twenty-four traps) there were likewise no significant changes in the total numbers caught or in the proportions of the two sexes in the catches, but the catches of males were much higher than those of females (significant in three trappings and only just short of the 0·05 level of probability in the fourth). There was, however, no significant deviation from the expected distribution of the frequency of captures, in either sex. For the males this may be evidence of real differences in behaviour between the stocks used in the various pens, as it repeats the result found in pen 2. For the females, on the other hand, it probably merely indicates the inadequacy of the data, for seven females died during the experiment, and owing to the general trap-proneness of the males, only six females were caught at each of the first three trappings, and only four at the fourth.

At this stage the experiments had to be discontinued, but as a number of pens were available, some of the males and females which had entered traps on every occasion in the last series were put together for breeding, and some of those which were either never or rarely caught were also mated. In these large pens, with no disturbance, the mice bred rapidly, and, after five months, stocks of sexually mature offspring of both trap-prone and trap-shy parents were available.

5. *Descendants of trap-prone parents and trap-shy parents*

Twenty-two females from trap-prone parents and 21 from trap-shy parents were released in a pen identical with those used previously, and allowed to settle down for some weeks (pen 7). They were then trapped overnight four times at intervals of fourteen days, with twenty-four traps.

There was little variation in the proportion of mice caught on the four occasions, undoubtedly due to the limited number of traps (23, 21, 21 and 22 mice respectively). When the captures are tested, there is evidence of heterogeneity in response to the traps (chi-square=62·97 with 42 d.f., P=<·05). When the captures are divided according to the origin of the mice, the figures are small, but significant deviation persists among the descendants of the trap-shy mice, although not among the others. (Table 8).

The most interesting result, however, was that at the first trapping, when trap-response was being tested free from the possible effects of experience, the catch of descendants of trap-shy mice was significantly lower (P=<·01). This difference was not evident at subsequent trappings.

Table 8—The frequency of capture of female descendents of trap-prone and trap-shy mice.

No. of captures	Trap-prone parentage		Trap-shy parentage		Total mice	
	No. caught	No. expected	No. caught	No. expected	No. caught	No. expected
0	1	0·9	3	1·7	4	2·6
1	6	4·5	7	6·0	13	10·5
2	6	8·1	4	7·8	10	16·2
3	6	6·5	4	4·5	10	10·9
4	3	2·0	3	1·0	6	2·8

Table 9—Numbers of trap-prone and trap shy descendents captured at each trapping.

Trapping	Caught		Not caught	
	Trap-prone	Trap-shy	Trap-prone	Trap-shy
1	17	6	5	15
2	12	9	10	12
3	9	12	13	9
4	10	12	12	9

DISCUSSION

Young *et al.* (1952) put forward as a possible cause of the heterogeneity in trap-response brought to light by their analysis, the relationship between home range and trap spacing. This must have been largely, if not completely, eliminated in these experiments, especially those in which excess traps were used. Their other suggestion, that the population contains trap-prone and trap-shy individuals has been borne out by our results.

There is some evidence, although it is by no means conclusive, that these differences in trap-response are due to inherent differences in temperament. It seems reasonable to suppose that wild house mice vary in their investigatory behaviour in a manner which can be measured by live-trapping, and that selective breeding over a number of generations might result in the production of strains exhibiting more marked differences in trap-response than those which can be detected in a wild population. Nevertheless, much of the heterogeneity in trap-response observed appeared to be a consequence of social strife. This effect may have been exaggerated by the experimental conditions. The absence of trap-proneness and trap-shyness in an all-female population, and their

appearance in these same females when males were present (pen 5) suggests that the effects of social strife may be marked, even in individuals not directly involved in it.

Andrzejewski *et al.* (1959) found a clear correlation between trap-proneness and social dominance among the males in confined colonies of laboratory mice. There was no evidence of heterogeneity in the trap-response of the females. The numbers of traps were small in relation to the numbers of mice, however, and captured mice were released before the next catch was taken. Thus the differences between their results and ours are likely to be due to differences in trapping and recording techniques, although differences in the behaviour of laboratory mice and wild mice cannot be ruled out as a contributory factor.

Young *et al.* (loc cit.) discussed the dangers of estimating population size using samples biased by heterogeneity in trap-response. Even in those pens in which the greatest heterogeneity was observed, the numbers of especially trap-prone or trap-shy individuals were not large, and the population estimates worked out from recapture data by means of the Lincoln index were surprisingly accurate. But these samples were much larger in relation to actual population size than those normally obtainable in the field. When the estimates are calculated from the catch taken early in the night (18.00 to 21.00 hrs) or from the catches limited by the numbers of traps, conditions which are more likely to simulate a practical situation, the proportion of trap-prone mice in the catch is usually high, and the estimates are accordingly too low.

The high catches at the first trappings in all pens shows that the wild house-mouse exhibits no general shyness of new objects, but, on the contrary, appears to be stimulated to investigate them (see also Crowcroft 1959). Although there was evidence of a slight fall-off in total catch in most pens, the probability of capture remained remarkably constant. On this evidence, therefore, the probability of recapture being the same as that of initial capture, the house-mouse would be classified with the brown rat (*Rattus norvegicus*) as " isoresponsive " if the terminology of Tanaka (1956) were adopted, in spite of the fundamental differences in the behaviour of the two forms.

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THE OCCURRENCE OF CURVED AND UNGULATE FORMS OF THE MUSSEL *MYTILUS EDULIS* L. IN THE BRITISH ISLES AND THEIR RELATIONSHIP TO *M. GALLOPROVINCIALIS* LAMARCK

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(With 2 plates and 3 figures in the text)

The discovery that mussels showing some features used to identify *M. galloprovincialis* Lmk. (the so-called " Mediterranean Mussel ") are more widespread in Britain than had previously been supposed, led to a re-appraisal of the distinction between this entity and *M. edulis* L. It is concluded that shell characters are too variable to afford a distinction between these two mussels ; the most reliable separating character appears to be the very dark colour of the mantle edge in mussels from the Mediterranean.

Curved and ungulate forms of British mussels are described and it is concluded that these are merely a form of *M. edulis*—probably the outcome of old age or slow growth. These ungulate mussels share similar shell characteristics with some populations of *M. galloprovincialis* ; also a very dark mantle edge may occur to some extent in populations of otherwise normal *M. edulis*. This intermingling of characters lends support to the taxonomic conclusion that *M. galloprovincialis* Lmk. cannot be regarded (on present evidence) as more than a race or subspecies of *M. edulis* L. In certain circumstances it appears to be impossible to distinguish between the two entities.

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INTRODUCTION

In a recent paper, Hepper (1957) records that the northern limit of *Mytilus galloprovincialis* Lmk. (the so-called " Mediterranean Mussel ") is to be found in south-west England and South Wales, and he summarizes the chief features in which this mussel, as found in Cornwall, differs from *M. edulis* L. Hepper

also mentions that some *M. galloprovincialis* had been found at Castletownbere (south-west Ireland) : and more recently Kitching *et al.* (1959) and Ebling *et al.* (1960) have recorded a similar mussel (again identified by Hepper as *M. galloprovincialis*) in Lough Ine in south-west Ireland. Presumably in consequence of Hepper's paper, *M. galloprovincialis* is regarded as a separate species also in the following recent publications : the latest edition of the *Plymouth Marine Fauna* (Marine Biological Association, 1957), Bassindale & Barrett (1957), Barrett & Yonge (1958), and Bassindale & Clarke (1960).

For some years we have been investigating the littoral ecology of sea-lochs in Argyll, Scotland (Lewis & Powell, 1960 a), in which local communities of large mussels occur in the lower part of the shore. Many of these mussels show shell features closely similar to those by which Hepper distinguished *M. galloprovincialis* in south-west Britain—in particular the pronounced and down-turned umbones. At first, we were inclined to regard their presence in Argyll as a consequence of the warm summer sea conditions in the lochs (for temperature data see Lewis & Powell, 1960 b) and as a demonstration of a northward extension in range of a southern species. However, a large proportion of mussels in these populations could not be adequately classified as either *M. edulis* or *M. galloprovincialis*. At the same time we began examining mussels from some other areas as opportunity arose, and have found similar shell forms at a number of localities, widely distributed in the British Isles and in diverse habitats. In all these cases the same difficulty of identification arose. This has led us to inquire into the diagnostic characters used by recent authors to distinguish the two entities, and we have found that there is little agreement either on this or on the taxonomic status of these forms.

THE DISTINCTION BETWEEN *M. GALLOPROVINCIALIS* AND *M. EDULIS*

The two most recent publications in which the distinction between these two mussels is considered in detail are those of Lubet (1959) and Hepper (1957). Lubet, working at Arcachon in the Bay of Biscay, but familiar with " *M. galloprovincialis* " from the Mediterranean (Lubet, 1957, p. 28), summarized the main distinguishing features in the following Table (on his p. 403), emphasizing in particular the importance of the last character :—

M. edulis	*M. galloprovincialis*
1. Région postérieure du manteau blanc-brunâtre.	Région postérieure du manteau noir-violacé.
2. Muscle adducteur antérieur petit et à insertion très latérale.	Muscle adducteur antérieur plus gros et à insertion moins latérale.
3. Coquille présentant des bandes violacées longitudinales (après avoir enlevé le périostracum).	Coquille de couleur homogène sans grosses bandes violacées.

Lubet states also (p. 440) that there are recognizable differences in the ratio of height to length and in the duration of the phases of the sexual cycle. There existed in his populations a small proportion (1–5 per cent) of " types intermédiaires ", that he interpreted as hybrids.

Hepper (1957) found that "*M. galloprovincialis*" from Cornwall differed from *M. edulis* in the following respects :

(i) umbones more pronounced, more pointed and down-turned ;
(ii) shells proportionately higher, giving a length/height ratio 1·77 compared with 1·95 for *M. edulis* ;
(iii) shells less angular, and the distinct angle between front and upper margins less evident ;
(iv) capable of growing to a larger size ;
(v) "mantle edge usually very dark, either blue, purple or violet, often appearing almost black", in contrast to the usual white to brown of *M. edulis*.

It will be noted that while these two authors agree on certain points (height of shell and colour of mantle edge), Lubet makes no mention of the umbone characters stressed by Hepper (nor do Lubet's photographs on his p. 402 show such characters at Arcachon), but he emphasizes the importance of the new criterion of longitudinal violet bands as opposed to homogeneous colouration of the shell. On the other hand, Hepper does not mention any differences in the size and position of insertion of the anterior adductor muscle. With regard to these muscle features, however, other opinions have been expressed : e.g. Bucquoy, Dautzenberg & Dollfus (1890, p. 139) refer to the small anterior adductor muscle scar in *M. galloprovincialis* (in the Mediterranean), and Soot-Ryen (1955, p. 20) also refers to the "higher, flatter forms with very small anterior adductor named *M. galloprovincialis* Lamarck in the Mediterranean and *M. diegensis* Coe in California".

Clearly the criteria used by Hepper and Lubet do not entirely agree and we should next consider whether any other authorities can contribute to any clarification of the characters of the Mediterranean Mussel widely referred to as *M. galloprovincialis* Lmk.* Bucquoy *et al.* (1890, p. 139) gave an amended diagnosis for *M. galloprovincialis* Lmk. referring to shell characters only. With regard to the anterior end of the shell they state "sommets terminaux, incurvés et un peu écartés" ; this we translate as "umbones terminal, incurved and a little apart". We are not certain of the precise meaning of "incurvés" for their photographs indicate that a slight down-curving of the anterior end of the shell may occur in some mussels ; but this can be a feature of the anterior end of the shell as a whole and not solely of the umbones. They further state that there is a well-marked angle at the junction of the dorsal and ligamentary (front) margins (such an angle is shown, for example, in our Pl. 1, fig. 3), and their photographs confirm this but also show several specimens in which the dorsal edge is much more rounded. In this and other shell characters it is clear from their description of several varieties that there is considerable variation in the form of this mussel in the Mediterranean, and they comment as follows upon the difficulty of distinguishing *M. galloprovincialis* from forms of *M. edulis* : "car il existe des formes étroites et allongées du *M. galloprovincialis* qui se rapprochent du *M. edulis* et des formes courtes et larges du *M. edulis* qu'il est difficile de distinguer du *M. galloprovincialis*".

* It should here be emphasized that, according to Lamy (1936, pp. 88, 91), *M. edulis* also occurs in the Mediterranean. In the present paper the term "Mediterranean Mussel" refers to populations of so-called *M. galloprovincialis* Lmk. ; see p. 594 for our conclusions concerning its taxonomic status.

A more complete description of the Mediterranean Mussel is given by List (1902) whose excellent illustrations (especially his Taf. 4) give a clear idea of the predominant form of shell at Naples. This is typically as shown in our Pl. 1, fig. 1 ; i.e. the shell is high, the junction of the dorsal and ligamentary margins is somewhat more angular than round, the postero-dorsal margin is rounded, the ventral margin of the shell is usually straight and the anterior end is pointed but with a slight bulbous swelling involving the hinge-plate, lunule, and possibly the umbone too (cf. List, Taf. 4, Figs. 5–7). Among the shell forms described and figured are some with a slight downward curvature of the anterior end of the shell (foreshadowing the down-turned umbones—or " beaking "—stressed by Hepper ?), and others in which the ventral margin curves sharply inwards before the hinge-plate swelling. The latter (List's Taf. 1, Figs. 14–21) have an outline similar to some specimens we possess from Scotland (see Pl. 2, fig. 20). A table of measurements on List's p. 16 indicates that the Naples mussel is narrow (i.e. not " fat "), the width/height ratio varying from about 0·6 to 0·7 (see also our Table 1). With regard to the anterior adductor scar, List remarks that it is small at Naples but quotes (p. 163) conflicting opinions whether this scar is larger than, or the same size as, in *M. edulis*. The colour of the mantle edge is described as brownish as a rule, except in some young individuals where it may be lighter, and figured as dark reddish-brown or purplish.

Further detailed information about shell proportions in the Mediterranean Mussel is given by Ricci (1957). His measurements indicate that " *M. galloprovincialis* " at Tunis is on average higher and narrower than *M. edulis* (from Germany) when large numbers are considered. He regards the difference in the length/height ratio as the principal difference between the two " species ".

We have obtained samples of mussels from Naples, Marseille and Monaco in the Mediterranean, and from Arcachon on the Atlantic coast of France (see Table 1 and Pl. 1). The Naples specimens (45 in our sample ; length of shell 3·5 to 5·9 cm.) all conformed very closely to the description of List, the main source of variation being in the length/height ratio (although all shells were high), and the more frequent angularity of the junction of the dorsal/ligamentary margins. In comparison with British mussels we were impressed by the brittleness of the shell, and the sharply pointed anterior end. The latter usually shows the hinge-plate swelling but no real beaking or downward curvature—certainly in no way comparable to that shown in Hepper's Pl. I and our Plates. The umbones are incurved (i.e. not divergent) as shown by List (Taf. 4, Figs. 1, 2). The mantle edge was the darkest in colour of any mussels we have examined so far ; they were a deep reddish-brown which looks purple as (usually) seen against the dark blue-black rim of the shell.

The specimens from Marseille are of particular interest in that they come from near the type locality for *M. galloprovincialis* Lmk. The type locality is stated by Lamarck (1819) to be near Martigues ; this is about 17 miles west of Marseille. Our sample of 108 specimens (length of shell 1·7 to 4·8 cm.) showed greater variation than the Naples sample in all shell characters. Thus, although the high and somewhat rounded shell persists, there are many with a very marked angle at the junction of the dorsal and ligamentary margins

Table 1—The ratio of length (L) and width (W) to height (H) in "*M. galloprovincialis*" and *M. edulis* from various sources.

Authority or locality	"*M. galloprovincialis*"					*M. edulis*				
	No. in Sample	L/H		W/H		No. in Sample	L/H		W/H	
		Mean	Range	Mean	Range		Mean	Range	Mean	Range
List (1902) (Naples)	17	1·80	—	—	0·60–0·70	—	—	—	—	—
Ricci (1957) (Tunis)		1·89	1·72–2·12	0·72	0·62–0·85	630*	2·19	—	0·83	—
Naples	45	1·85	1·65–2·11	0·71	0·60–0·79	—	—	—	—	—
Marseille	108	1·81	1·50–2·10	0·73	0·57–0·92	—	—	—	—	—
Monaco	55	1·94	1·79–2·21	0·70	0·63–0·78	—	—	—	—	—
Millport	—	—	—	—	—	367	1·94	1·55–2·30	0·72	0·57–0·85
Hepper (1957) (Padstow)		1·77	—	—	—		1·95	—	—	—

* It is not clear from Ricci's text where these *M. edulis* were collected, but we infer that they were sent to him from Germany.

and in these the dorsal and ventral margins of the shell frequently lie parallel giving a quadrilateral appearance more frequently than in the Naples sample (see Pl. 1, fig. 3). In most cases the hinge-plate swelling is slightly more prominent than in the Naples mussels, and in about 5 per cent of the sample is accompanied by from slight to marked downward curvature of the umbones and anterior end, and where these latter features are most developed the umbones are also divergent. The colour of the mantle edge was again dark reddish-brown.

The mussels from Monaco (55 in the sample ; length of shell 5·6 to 8 cm.) were generally similar to those from Naples, but the majority were inclined to have more parallel-sided upper and lower edges. The hinge-plate swelling was usually prominent and, when the ventral edge was straight, the swelling resulted in a slightly beaked appearance. There was no real beaking of umbones or curvature of shell ; in many cases the ventral edge curved up at the anterior end. Slight divergence of the umbones occurred in many specimens. The mantle edge was dark reddish-brown. The shells were thinner and more brittle than in British *M. edulis* of comparable size.

The sample from Arcachon agreed largely with Lubet's description of *M. galloprovincialis* from this locality. It must be emphasized, however, that the shape of Arcachon shells (as shown in Lubet's Fig. 2, and our Pl. 1, fig. 4) widens further the range of shell-shape found in mussels referred to *M. galloprovincialis*.

We should now consider which, if any, of the characters variously attributed to *M. galloprovincialis* are sufficiently constant to distinguish it from *M. edulis* as found in the British Isles.

1. *Shell characters*

(*a*) *Height*. Table 1 shows the relationships of length and width to height, compiled from various sources. In general, *M. galloprovincialis* in the Mediterranean appears to be higher relative to length than is *M. edulis*, but less so than reported by Hepper for the Padstow (Cornwall) population of *M. galloprovincialis*. However, Table 1 also shows the very wide (and similar) *range* of ratios in both *M. galloprovincialis* and *M. edulis*, and when in addition some samples revealed that the length/height ratio increased as a function of length (age ?), it appears that the length/height ratio is a character of doubtful validity for identification purposes, and certainly could have no reliability for individual specimens.

An appearance of greater height in *M. galloprovincialis* may result from the narrowness (small width) of some of the animals. Thus, from Ricci's data, it appears that this mussel has a lower width/height ratio (mean 0·72) than has *M. edulis* (0·83). Lubet, however, states (p. 409) that at Arcachon there is no difference in width relative to height, and our samples support this view. Thus our *M. galloprovincialis* from Naples, Marseille and Monaco average 0·71, against 0·72 for *M. edulis* from Millport. As with the length/height ratios, the width/height ratios have a considerable range : 0·57–0·92 for *M. galloprovincialis* and 0·57–0·85 for *M. edulis*.

(*b*) *Angularity of the ligamentary/dorsal margins.* The variation of this character (in *M. galloprovincialis* from all sources), ranging from sharp-angled parallel-sided forms to those with a smoothly rounded upper margin, makes it valueless for identification purposes.

(*c*) *Shape of anterior end :*

(i) *Pointed or rounded.* In view of the fact that most illustrations and many of our specimens of *M. galloprovincialis* from the Mediterranean show a relatively sharply pointed anterior end, we investigated whether this character might afford a means of separating this entity from *M. edulis.* While many British *M. edulis* do have blunter anterior ends, associated with a generally thicker shell, these appear to be mainly older individuals and the younger quickly growing animals frequently have shells as sharply pointed and thin as Mediterranean Mussels of comparable size.

(ii) *Hinge-plate swelling.* The prominence of this regular slight swelling in the Mediterranean Mussel is caused by slight indentation of the ventral margin immediately behind the thickened hinge-plate and lunule and is accentuated by the thinness of the shell. *M. edulis* can also show this feature but it is often less noticeable because of the thicker shell and blunter anterior end.

(iii) *The umbones and curvature.* The hinge-plate swelling may be accompanied in *M. galloprovincialis* by slight divergence and downward curvature (beaking) of the umbones and by downward curvature of the entire anterior end of the animal, but these characters are not sufficiently common to characterize any whole sample and are therefore not diagnostic.

(*d*) *Anterior adductor muscle scar.* Most authors agree that this scar is relatively very small in the Mediterranean Mussel. Lubet, however, stresses that the anterior adductor muscle is larger in his *M. galloprovincialis* than in *M. edulis* at Arcachon. This is contrary to our findings in comparing the Mediterranean Mussel with British *M. edulis,* but we do not wish to stress this point because it is a difficult character to observe and assess. Neither can we find any regularly significant difference in the position of the muscle-scar (cf. Lubet).

(*e*) *Shell colour.* Mediterranean Mussels of the blue-black type appear to lack coloured striations, but the pale forms illustrated by List (Taf. 1) show marked striations. British *M. edulis* may or may not show striations, and therefore their presence or absence is not a differentiating criterion.

2. *Mantle edge colour*

Apart from List's reference to the pale colour in some young individuals, the dark brownish-purple colour of the mantle edge appears to be a constant character of the Mediterranean Mussel.

3. *Duration of phases of the reproductive cycle*

According to Lubet, the duration of the reproductive cycle in *M. edulis* at Arcachon is slightly shorter than that of " *M. galloprovincialis* " growing in the same situations. Berner (1935) found that *M. edulis* at Calais had a shorter reproductive period than *M. galloprovincialis* in Provence ; but small

differences in reproductive cycles at localities so far apart would appear to be a doubtful criterion by which to distinguish species.

We conclude that the only constantly occurring distinguishing character for the separation of *M. galloprovincialis* from *M. edulis* is the *darker coloured mantle edge*.

Less reliable, but possibly valid with large populations, are :

(i) greater length of the reproductive cycle (but obviously this is not a criterion of practical value for field identification) ;
(ii) shell height in relation to length ;
(iii) prominence of the hinge-plate ;
(iv) thinness of the shell.

Characters too variable or otherwise unsuitable to afford distinction from *M. edulis* include :

(i) pointed anterior end ;
(ii) divergence and down-turning (beaking) of the umbones, and downward curvature of the anterior end of the shell ;
(iii) angularity at the junction of the ligamentary and dorsal margins ;
(iv) striation of the shell ;
(v) size and position of the scar of the anterior adductor muscle.

DESCRIPTION OF SOME UNUSUAL MUSSEL POPULATIONS IN THE BRITISH ISLES

As stated in the Introduction, it was the presence of prominent down-turned umbones in mussel populations far removed from south-west England that first stimulated us to look at mussels in a number of different environments, and this led to the discovery of several additional characters which appear to have been largely overlooked in the past. The types of environment investigated ranged from very sheltered sea-lochs in Argyll to open surf-swept shores in the west of Ireland and north-east England.

The characters to which we shall now draw attention may occur singly or all together or in various combinations in individual mussels. They may be feebly or strongly developed, but strong development of one character tends often to be accompanied by strong development of the others. This final stage produces a most distinctive mussel which, to the best of our knowledge, has not been adequately described before, and which would scarcely be recognized as *M. edulis* as widely understood.

1. *Shape of anterior end.* The umbones, which are usually close together in *M. edulis*, diverge to give a pronounced V- or U-shaped groove between them (see Pl. 1, especially figs. 7, 8, 9, 12, 13, 15, and Pl. 2, figs. 16–19, 21). Accompanying the divergence there may be a general downward curvature of the anterior end of the shell and especially of the umbones, which we call beaking. This beaking, together with thickening of the shell, obscures any hinge-plate swelling there may be. It may also produce in some specimens a very sharp anterior end in external view and, because this is primarily caused by the umbones, the junction of the ventral and ligamentary edges (in inner surface view) tends to remain less sharp than in *M. galloprovincialis*.

2. *Curvature.* The beaking often develops into a curvature involving most of the ventral surface and this is accompanied by complete curvature of the

dorsal/ligamentary margins. This process results ultimately in a shallow reniform profile such as is shown in Pl. 1, fig. 9. The curvature of the ventral surface may be accompanied or replaced by a distinct angle about one-quarter along the ventral margin from the anterior end (Pl. 2, fig. 22). Where ventral curvature is not great the upper surface curves gradually throughout (Pl.1, fig. 15).

3. *Width/height ratio.* In "normal" *M. edulis* the width/height ratio varies between about 0·6 and 0·85. In our specimens the divergence of the umbones is accompanied by a general lateral bulging giving width/height ratios of about 0·8 to 0·95, and when in addition marked dorsi-ventral flattening develops (see Pl. 2, fig. 19) the ratio may become as high as 1·2 or even 1·3 in extreme cases. Thus these mussels are fat rather than high (Pl. 1, figs. 8, 9). In cases of extreme flattening the dorsal and ventral edges of the two valves meet in the horizontal plane and may even become slightly inturned on the ligamentary and ventral edges.

The varying development and combinations of the features 1–3 above account for the range of shell shapes such as are shown in our Plates 1 and 2. Thus divergence, beaking, and curvature which are not accompanied by dorsi-ventral flattening produce high, rounded and fat mussels (Pl. 1, figs. 12, 13). Flattening and divergence without over-all curvature give a long broad animal which may or may not be slightly beaked (Pl. 1, fig. 15). In all populations showing the extreme development of these various characters there are all transitional forms back to normal *M. edulis*, and indeed the most frequent form of expression especially in the loch samples is only a slight beaking or divergence of the umbones, with curvature of the dorsal surface (Pl. 2, figs. 16–18).

The greatest contrast with these curved forms is provided by specimens in which the anterior end curves the other way (Pl. 2, fig. 20) ; such specimens usually have umbones close together, but a few were found with divergent umbones.

The distinctive characters described above have now been found well developed in specimens from among populations in the following localities :

Argyll, Scotland : Loch Sween, including Linne Mhuirich ; West Loch Tarbert ; Loch Craignish ; Loch Melfort—all very sheltered sea-lochs.

West of Ireland : Cream Point and Carrowmore Point (Co. Clare) ; and a point midway between Slea Head and Ventry Harbour in Co. Kerry—exposed and semi-exposed open coasts.

Yorkshire : Ravenscar and Robin Hood's Bay—exposed and semi-exposed localities respectively.

Slight development of these characters, mainly beaking, has been found in a few specimens in samples from :

East coast : St. Andrews ; Blyth Harbour (Northumberland).

Argyll, Scotland : Point of Knap.

Wales : Aberystwyth.

None of these features has yet been found in samples from Millport, or from Filey Bay and Filey Brig (Yorkshire).

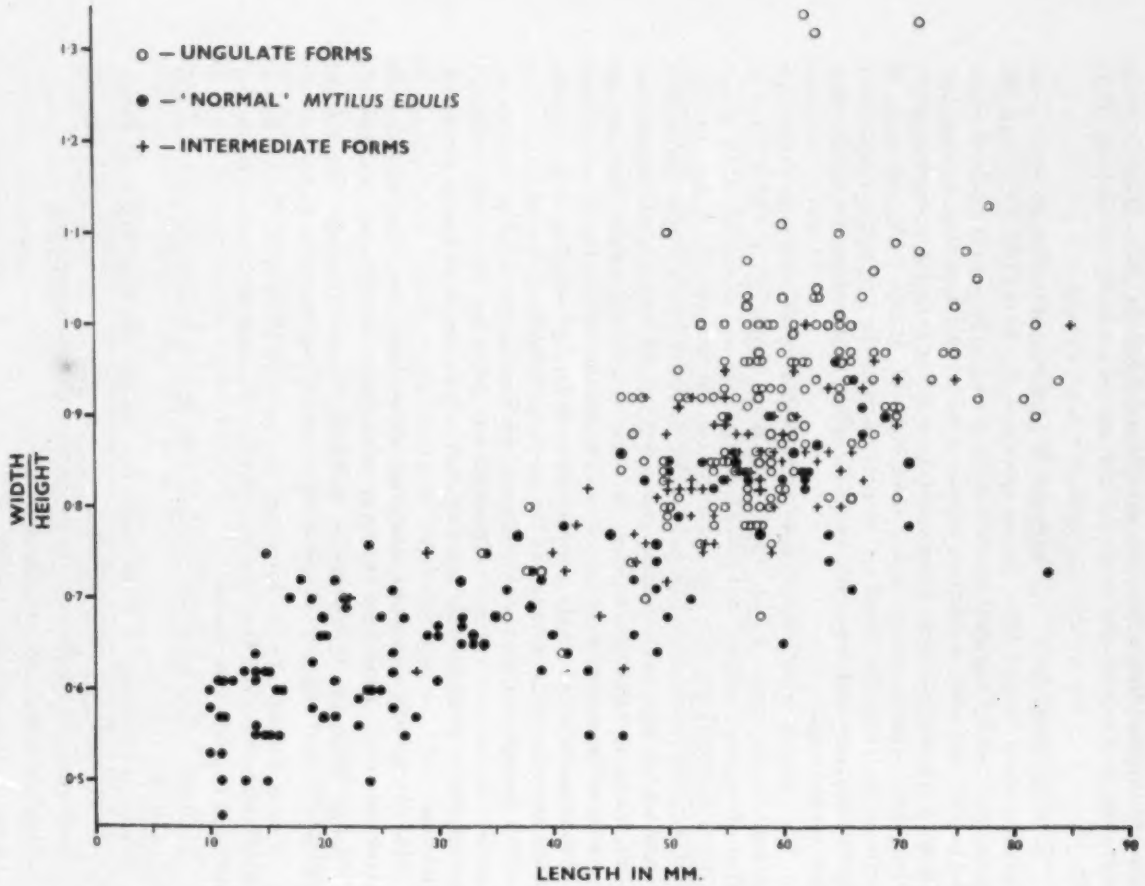

Fig. 1—The presence of ungulate characters and the relationship between width, height and length in a random sample of 362 mussels collected from the lower shore of Linne Mhuirich, a very sheltered arm of Loch Sween in Argyll, Scotland.

It appears from analysis of the samples from the sheltered Scottish lochs, and the exposed and semi-exposed shores of western Ireland and Yorkshire, that the maximum expression of these shell characters is to a large extent a function of age. This is brought out in Fig. 1 (lochs) and Figs. 2, 3 (open coasts). In these analyses the samples were divided as far as possible into two groups—" normal " and " ungulate ". The ungulate* category included all specimens showing beaking, curvature, and/or divergence of the umbones, except in the few cases where the latter occurred with a marked upward curvature of the anterior end. However, from 12 to 22 per cent of each sample were unclassifiable even in this arbitrary way ; these are included in the figures as " intermediate forms ". We have chosen to illustrate these populations by reference

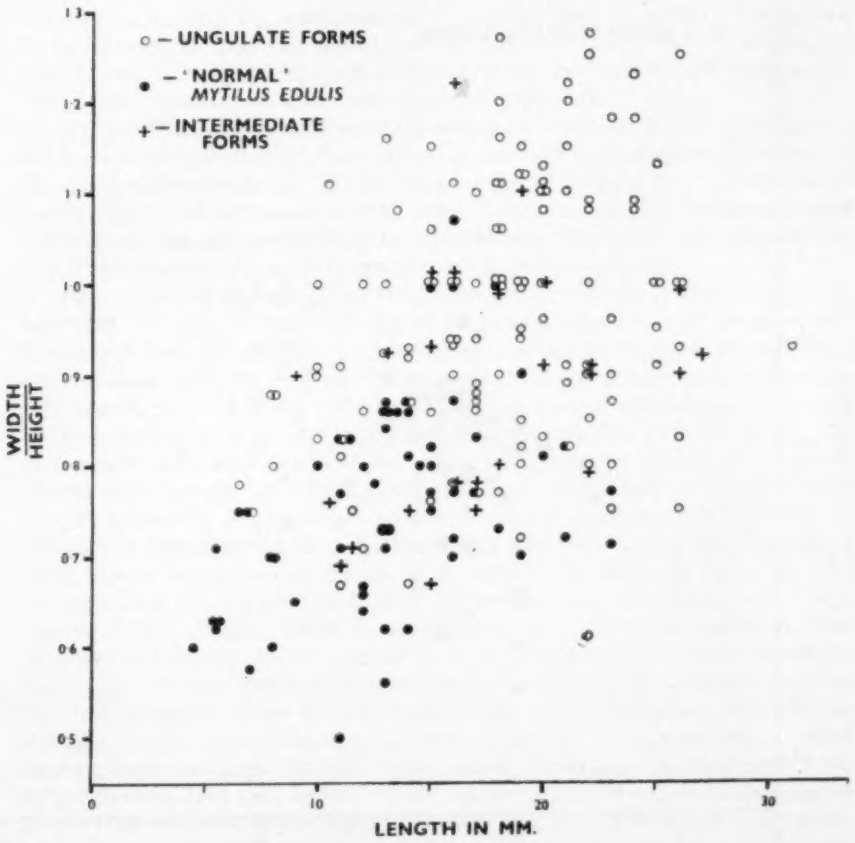

Fig. 2—The presence of ungulate characters and the relationship between width, height and length in a random sample of 217 mussels from above M.T.L. on exposed open coasts in Co. Kerry and Co. Clare, Ireland.

* I.e. claw-like, having down-turned and divergent umbones.

to the width/height ratio since a high value invariably results from the divergence of the umbones coupled with lateral bulging and dorsi-ventral flattening, and these characters themselves may be accompanied by beaking and curvature. In cases where beaking and divergence of the umbones are not accompanied by flattening, the ratio does not, of course, give such high values. The three figures show that normal individuals can be found at all sizes and that a few which are old and large have a high width/height ratio too,

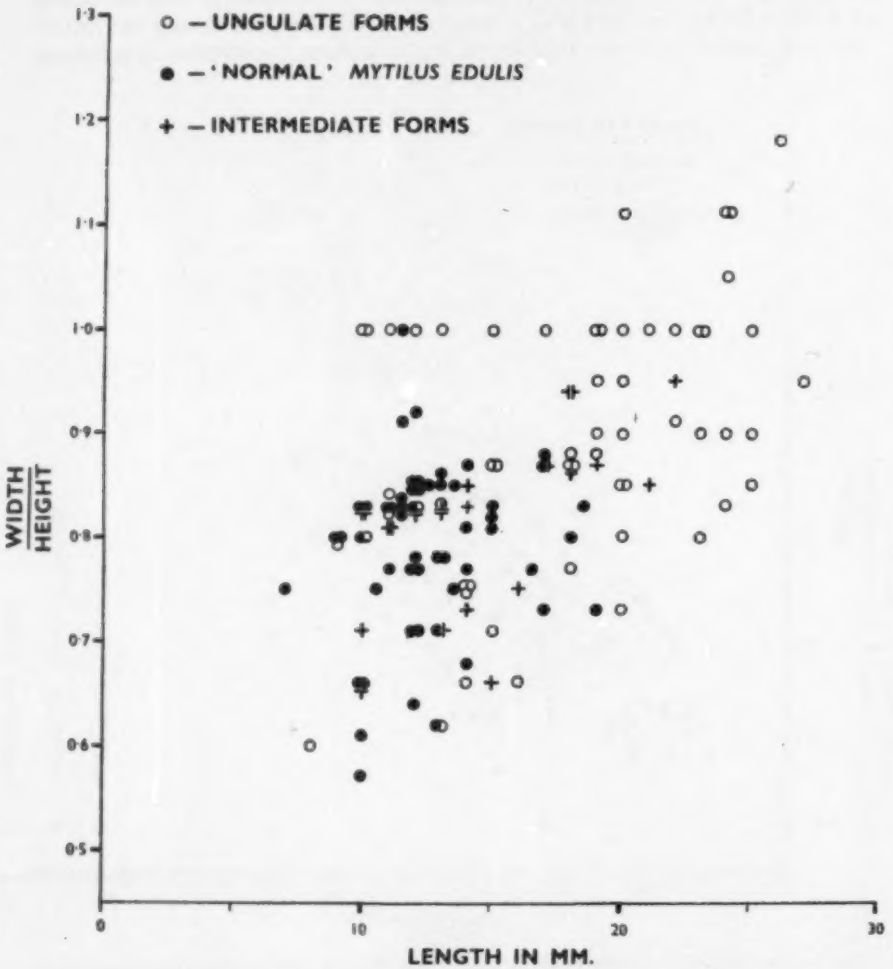

Fig. 3—The presence of ungulate characters and the relationship between width, height and length in a random sample of 133 mussels from above M.T.L. on an exposed open coast at Ravenscar, Yorkshire.

but the ungulate category predominates in the larger specimens (with eroded shells), and indeed in the loch samples we have yet to find an ungulate mussel much below 30 mm. long. The much smaller maximum length in the open coast samples is explained by the fact that they came from the upper midlittoral where the growth rate is very much slower than in the lower shore of the lochs. The restriction of ungulate characters to the larger specimens is less marked here but nevertheless we are satisfied that they occurred mainly in individuals whose gnarled eroded shells with many growth lines suggested that they were of considerable age.*

TAXONOMIC STATUS OF THE UNGULATE FORMS

In order to decide the taxonomic status of these unusual but obviously widespread mussels we must consider (i) whether they are akin to the mussels in south-western England referred to as "*M. galloprovincialis*" by Hepper (1957), and (ii) whether the latter accord with our conception of *M. galloprovincialis* Lmk. from the Mediterranean (see pp. 584–588).

To take the second question first, Hepper's mussels, in that they have a dark coloured mantle edge, have the only constant distinguishing character of *M. galloprovincialis* Lmk. Some further support is provided by the length/height ratio of his specimens and the pointed anterior end, but the down-turned umbones (which are also slightly divergent in his Plate) although known from the Mediterranean are not a diagnostic feature of this mussel.

Our ungulate mussels share with Hepper's only the down-turn of the umbones, but this is not a feature of *M. galloprovincialis*, and all our other characters (overall curvature, flattening, marked divergence of umbones, width/height ratio, etc.) are even further removed and merge by all gradations into normal *Mytilus edulis* with which they are always associated. The colour of the mantle edge is darkest in our loch samples and that from Co. Kerry, but it is never more than dark brown. Moreover, a range from dark brown to almost white occurs in both the ungulate and normal forms ; this is normal for *M. edulis* L. Therefore on no count can our specimens be regarded as having the characters of *M. galloprovincialis* and we conclude that we have a little known but widespread form of *M. edulis*. Possibly we have here the *M. ungulatus* of Linnaeus that most authorities (e.g. Bucquoy *et al.*, 1890 ; Lamy, 1936 ; Dodge, 1952) have regarded as a distorted specimen best disregarded for purposes of nomenclature, but several past records for which from south-western England Hepper has included in his *M. galloprovincialis*. On shell characters alone we can visualize that some of Hepper's *M. galloprovincialis* would be indistinguishable from those in our samples which show beaking and curvature without dorsi-ventral flattening. In such cases the only difference between the two would appear to be the colour of the mantle edge. This can be an exceedingly subjective and difficult criterion to use when comparing the darker specimens of *M. edulis* with *M. galloprovincialis*, and

* It is interesting to note that, for the "var. *herculea* Monterosato" of *M. galloprovincialis* Lmk., Bucquoy *et al.* (1890, p. 140) report that "les sommets deviennent saillants et aigus avec l'âge" (the umbones become projecting and pointed with age), adding that this is not noticeable in young mussels.

indeed certain of our specimens from the Scottish lochs and from Kerry could not be satisfactorily identified by this means.

Allowing that a form of "*M. galloprovincialis*" may occur in British waters, it nevertheless appears from Hepper's account to have developed the anterior beaking of some forms of *M. edulis*; indeed this feature occurred also in a small percentage of our sample from Marseille. Also, as we have stated, a very dark mantle edge occurs to some extent in normal *M. edulis*. This intermingling of characters lends support to the taxonomic conclusion of several other recent workers that *M. galloprovincialis* Lmk. cannot be regarded (on present evidence) as more than a race or subspecies of *M. edulis* L.—see, e.g., Bouxin (1956; and in Lubet, 1957), Soot-Ryen (1955), Dodge (1952).

What we particularly wish to draw attention to at this stage is the widespread occurrence of beaking, of divergent umbones and/or curvature in *M. edulis* (particularly in older specimens) that might lead to, in our view, erroneous identification as *M. galloprovincialis*.

It would be particularly interesting to know the geographical range through which these characters of *M. edulis* may be found, and we hope to extend this inquiry to other parts of the British Isles and the North Atlantic generally.

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SUMMARY

The discovery that mussels showing some of the features used to identify *M. galloprovincialis* Lmk. (the so-called "Mediterranean Mussel") are more widespread in Britain than had previously been supposed, led to a re-appraisal of the distinction between this entity and *M. edulis* L.

A consideration of the literature and examination of specimens obtained from the Mediterranean revealed considerable variation in Mediterranean Mussels themselves and led to the conclusion that shell characters are too variable to distinguish these from *M. edulis*; the most reliable separating character appears to be the very dark colour of the mantle edge in mussels from the Mediterranean.

Curved and ungulate forms of British mussels are described and it is suggested that these may be the *M. ungulatus* of Linnaeus.

Lacking regular development of a dark mantle edge, and showing all intermediate shell shapes back to "normal" *M. edulis*, it is concluded that these ungulate mussels are merely a form of *M. edulis*—probably the outcome of old age and/or slow growth.

These ungulate mussels share similar shell characteristics with some populations of *M. galloprovincialis*; also a very dark mantle edge may occur to some extent in populations of otherwise normal *M. edulis*; this intermingling

of characters lends support to the taxonomic conclusion of several other recent workers that *M. galloprovincialis* Lmk. cannot be regarded (on present evidence) as more than a race or subspecies of *M. edulis* L. In certain circumstances it appears to be impossible to distinguish between the two entities.

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NOTE ADDED IN PROOF

Since this paper was written, we have found curved and ungulate *Mytilus edulis* in samples from the following additional localities : (i) on open coasts in South Wales (Gower peninsula), the Channel Islands (Guernsey), in the N.W.

part of the Mainland of Orkney; and (ii) at sheltered sites in Scandinavia (Gullmarfjord, Hardangerfjord, near Espegrend, Trondheimsfjord, and near Bodö). In some of the Scandinavian samples, the mantle edge of some mussels was very dark in colour.

EXPLANATION OF THE PLATES

Plate 1

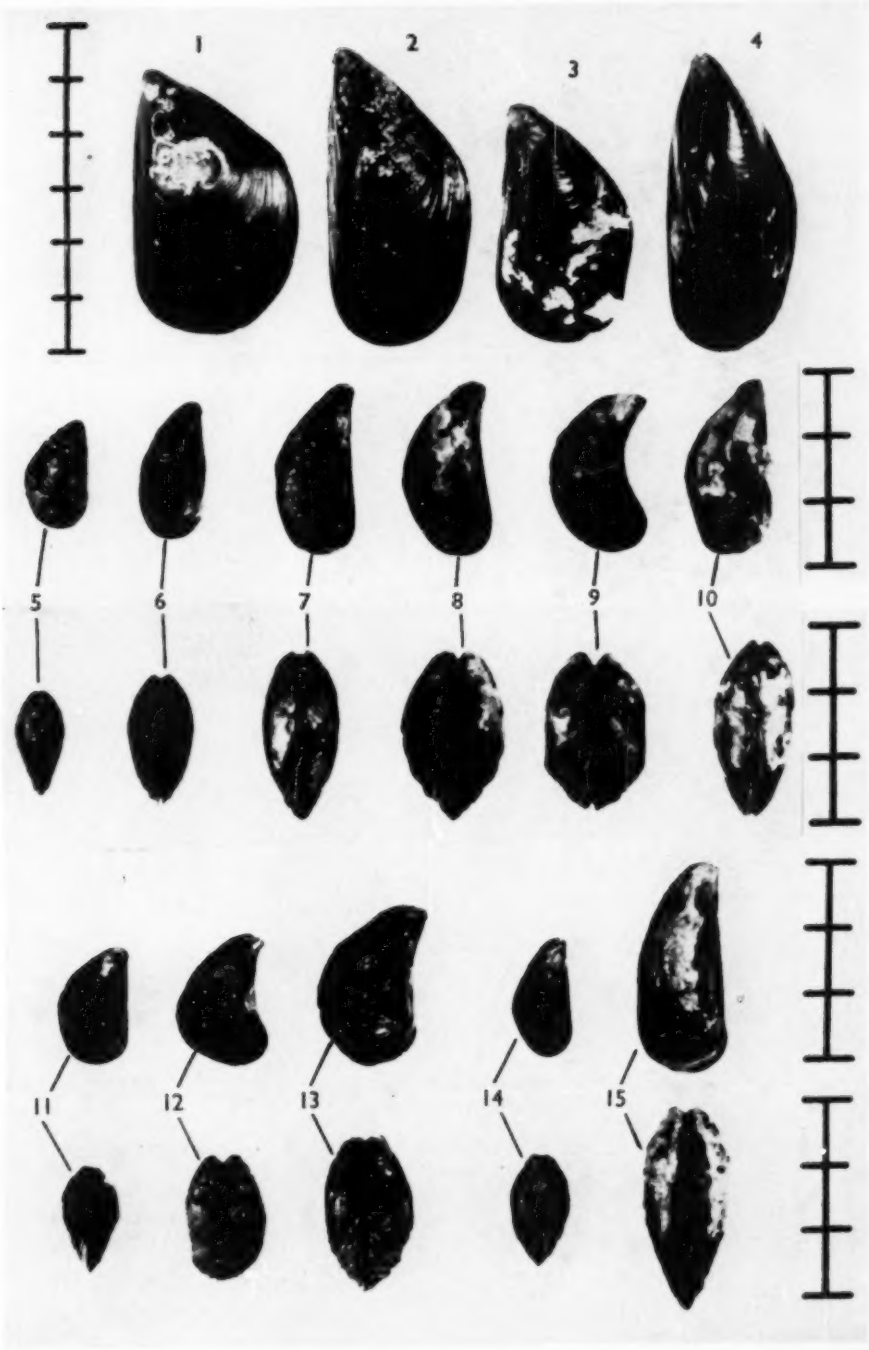
Figs. 1–4—"*Mytilus galloprovincialis* Lmk."
1 and 2 from Naples; 3 from Marseille; 4 from Arcachon. Side views.

Figs. 5–15—*Mytilus edulis* L. from mid-shore levels on exposed and semi-exposed shores of the British Isles.
5–9 from Cream Point, Co. Clare; 10 from near Slea Head, Co. Kerry; 11–13 from Robin Hood's Bay, Yorkshire; 14 and 15 from Ravenscar, Yorkshire. Side and (antero-) dorsal views.

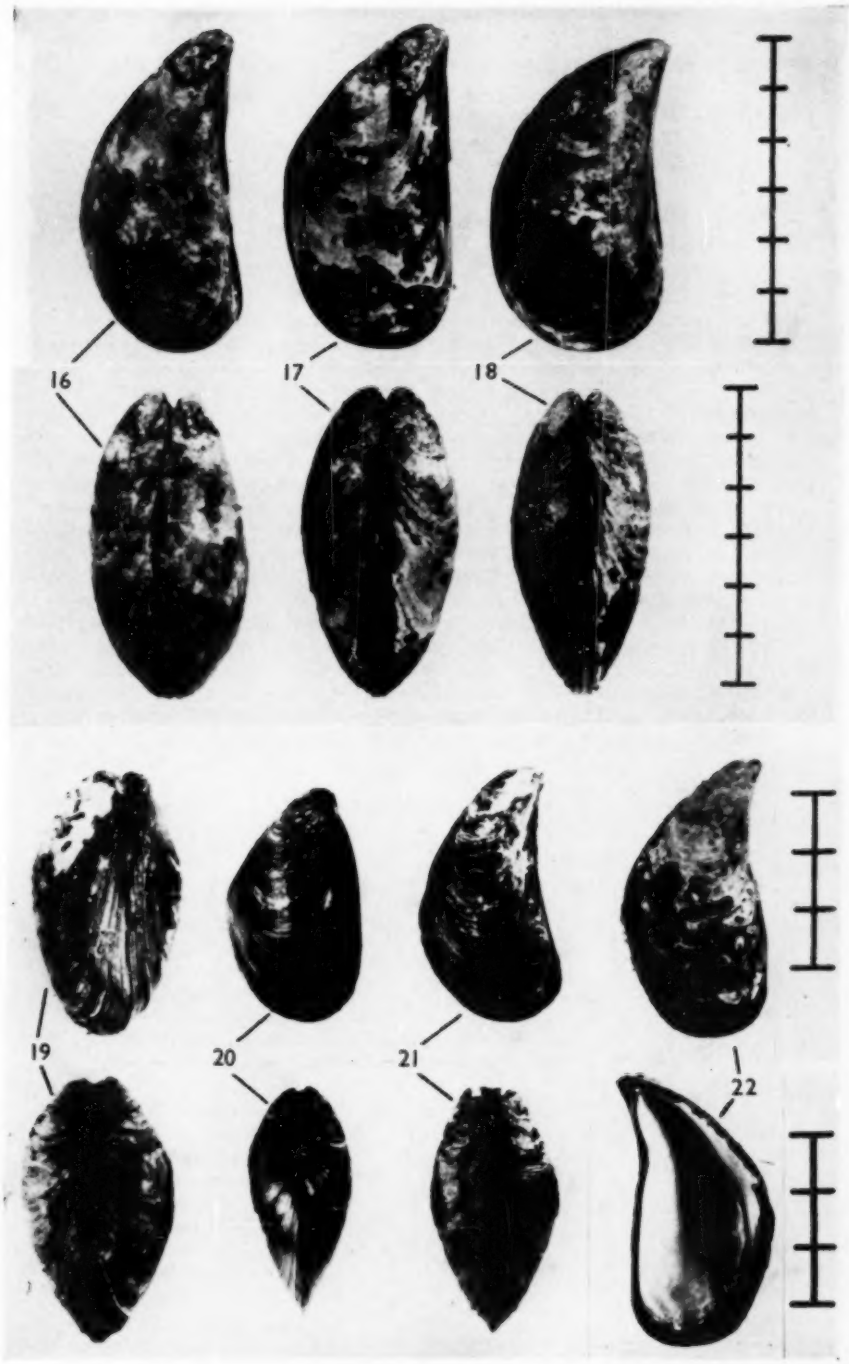
Plate 2

Figs. 16–22—*Mytilus edulis* from low tide levels in sheltered lochs in western Scotland.
16 and 22 from Linne Mhuirich; 17 and 18 from West Loch Tarbert; 19 from Loch Craignish; 20 and 21 from Loch Sween. Side and (antero-) dorsal views of 16, 17, 18, 20, 21; ventral and (antero-) dorsal views of 19 to illustrate the great width, and the marked flattening of the ventral surface, of this specimen; side and inner surface views of 22.

Scales throughout show cm.



Figs. 1–4—"*Mytilus galloprovincialis* Lmk."
Figs. 5–15—*Mytilus edulis* L.



Mytilus edulis from low tide levels in sheltered lochs in western Scotland.

ON THE FOOD OF THE BROWN TROUT OF LLYN TEGID

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(With 1 figure in the text)

The composition of the diet of Llyn Tegid trout has been determined by analysing the stomach contents, using the volume, number and occurrence methods. All three methods yield comparable results, but the volume method is the most satisfactory. The trout is an indiscriminate carnivore. The relative extent to which different animals are eaten depends mainly on their numerical representation in the fauna, though their size, habits and mobility are probably also important. In Llyn Tegid, *Gammarus pulex* formed 24 per cent by volume of the total food consumption. Other important animals were the caddis larvae *Limnephilus lunatus* and *Potamophylax stellatus*, the mayflies *Ephemera danica* (especially the sub-imago) and *Leptophlebia marginata* (nymph) and the isopod *Asellus meridianus*. Seasonal changes in the diet were considerable and appeared to be largely the result of seasonal changes in the availability of the different food organisms. From October to April, the trout fed mainly on bottom-living organisms, and from May to September on animals caught at the surface. The mean volume of food eaten increased greatly in summer to a mid-summer peak more than eight times the winter level. This was probably due to seasonal physiological changes in the trout and to a spring and summer increase in the amount of available food. A comparison of the caddis larvae eaten by the two fishes indicates that the trout is a more superficial feeder than the grayling. It is suggested that this reduces competition for food between the two species. In accordance with the findings of other workers, the trout appeared to avoid eating corixids. No important change in feeding-habits with size was found within the size-range covered by the samples (88–344 mm.), all the trout being in the insect-feeding stage.

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INTRODUCTION

This paper is an account of some results of a survey of the biology of trout in a Welsh lake. A general introduction to the survey and an account of the trout growth has already been published (Ball & Jones, 1960). The present paper deals with information about the food of the trout derived from examination of stomach contents, and includes a discussion of some of the problems arising from the work on food and growth.

The literature on the food of brown trout is enormous, including many reports in angling journals about feeding habits in different localities. A generalisation that emerges from consideration of previous work is that the extent to which trout feed on any particular food organism depends mainly on its accessibility and representation in the fauna, these factors alone accounting for the composition of the diet without involving discrimination by the fish (Pentelow, 1932 ; Slack, 1934 ; Neill, 1938 ; Frost, 1950 ; Allen, 1951 ; Frost & Smyly, 1952 ; Nilsson, 1955 ; Stube, 1958). This principle of opportunism has been qualified by some workers (Allen, 1938 ; Frost, 1939, 1945), who thought that though the composition of the diet broadly reflects the faunal make-up, some selection is exercised by the trout, although Allen (1951) could find no evidence of selection in his very full New Zealand study. A further point of some importance is that as the trout grows it takes bigger food organisms, the larger fish tending to be exclusively piscivorous (Allen, 1938, 1951 ; Swynnerton & Worthington, 1940 ; Butcher, 1945 ; Nilsson, 1955). Seasonal dietary changes appear to be determined by changes in the availability and size of the food organisms (Allen, 1938 ; Nilsson, 1955).

Apart from the work on the brown trout, important information on the feeding of the ecologically similar salmon parr comes from Carpenter (1940) and Allen (1940, 1941 a).

MATERIAL

Stomachs were taken from trout caught at all times of the year in routine shore nettings. A total of 253 stomachs were examined, grouped in monthly samples as follows : December, 1952–34 ; January, 1953–29 ; February—10 ; March—60 ; April—29 ; May—13 ; June—28 ; July and August (combined sample)—11 : September—19 ; October—20. No samples were available for November. In each monthly sample, stomachs were used from all the regular netting stations (Ball & Jones, 1960) to minimise feeding differences resulting from local faunal peculiarities. All the trout were caught between 12.00 noon and 5.00 p.m. so effects due to diurnal variations in feeding were avoided. The stomachs were preserved in the field in 10 per cent formalin and brought back to the laboratory for examination.

METHODS

Hynes (1950) has classified and described the different methods of gut examination that have been used to study the food of fishes, and with this review as a guide various methods were tried out on trout stomachs and modified where nesessary. The method finally applied to each monthly sample involved estimating the degree of fullness of each stomach, counting

the individuals in each food category, determining the average volume of the individuals of each category, and hence the total volume of the category by multiplying the average individual volume by the number of individuals counted. The percentage composition of the diet in each month could then be expressed in terms of the number of individuals in each food category (" number method "), the total volume of each food category (" volume method "), and the number of occurrences of each food category in all the stomachs examined (" occurrence method "). The degree of fullness of the stomachs and the mean volume of food per stomach each month provided ways of following seasonal changes in the amount of food eaten.

Only the stomach contents were examined since food beyond the pylorus was usually greatly digested. To make the counts comparable it was necessary to ensure that the same anatomical features were used to delimit the stomach in every fish. The pylorus in the trout gut is an obvious constriction marking the distal limit of the stomach, but the boundary between the stomach and oesophagus is not readily apparent. Accordingly, in each case a cut was made across the pylorus and continued across the adjacent cardiac limb of the stomach to give a U-shaped " standard " stomach. Only contents of the " standard " stomach were sorted, except when the trout had eaten a fish. The fish usually lay largely in the oesophagus, but was included in the stomach contents.

Degree of fullness of the stomach

The stomachs were classified as follows :

Empty	Stomach collapsed, no food present.	0 *points*
¼ *Full*	Food occupying about one quarter of the total volume of the stomach. Wall feels thick and hard when pressed between forceps.	1 *point*
½ *Full*	Stomach containing food, generally along most of its length, but the inner surface is longitudinally pleated and the wall feels thick and hard between forceps.	2 *points*
¾ *Full*	Stomach nearly filled with food, but some space remains and a small region of the wall feels thick and hard, with shallow longitudinal pleats internally.	3 *points*
Full	Stomach full. Internal longitudinal pleats shallow or absent. Entire wall feels soft and can be indented with forceps in the intact stomach.	4 *points*
Distended	Stomach packed with food. Wall cannot be pinched with forceps in the intact stomach, and is thin and stretched with no internal pleating.	5 *points*

Each category was awarded points, as indicated, and for each monthly sample the mean number of points per stomach was calculated. The resulting figure is termed the *fullness index*.

Numerical counts

After assessing the degree of fullness of a stomach, all the contents were transferred to 30 per cent alcohol and the various organisms sorted and counted, using a low-power binocular microscope.

Bottom-living animals were identified to species as far as possible, to permit comparison of their occurrence in the trout diet with their representation in the fauna as determined by Dunn (1952). Aerial insects were usually identified as far as orders and no further. Specific identification of unimportant dietary items (e.g. larvae of Coleoptera) was not attempted.

Some organisms (e.g. *Gammarus pulex*, *Asellus meridianus*) were often found in large numbers. Their number was estimated by placing them in a petri dish on a sheet of graph paper and arranging them in a single compact layer, so that as far as possible all individuals touched their neighbours and left no space between them. The area covered by this layer of animals was then determined, together with the average number of individuals covering a suitable unit area. The total number of individuals present could then be derived by simple proportionality.

When food animals were broken by digestion, the heads in each food category were counted. A possible result of this is that insects with hard head capsules resistant to digestion (e.g. larval Trichoptera) were overestimated in comparison with animals such as *Asellus meridianus*, in which the head is no more resistant to digestion than the body. However, the effect could only be slight in comparison with the total number of organisms counted, since digestion had rendered this method necessary in only a few stomachs.

Volume determination

For the main food categories, the total volume eaten each month was estimated. As many as possible average-sized intact individuals of each category were collected and their volume determined by water-displacement in a burette. Knowing the number of individuals counted for the month, the total volume of the food category consumed in the month was calculated. Specimens sometimes had to be taken from sources other than trout stomachs to obtain enough individuals for accurate determination of their volume, either from general faunal collections or from the stomachs of grayling caught at the same time as the trout. Care was taken to ensure that the specimens used were of the same size as those in the trout stomachs. The method resembles that used by Neill (1938) to determine the total weight of each food category eaten by trout.

For each month, application of the above methods gave the following information :

1. The percentage composition of the diet by number, volume and occurrence.

2. The percentage number of stomachs that were Distended, Full, $\frac{3}{4}$ Full, $\frac{1}{2}$ Full, $\frac{1}{4}$ Full and Empty, and the monthly fullness index.

3. The mean volume of food and mean number of food animals per stomach.

LIST OF FOOD ORGANISMS

(i) *Bottom fauna*

Annelida

**Erpobdella octoculata* Linn.

Mollusca

**Limnea pereger* Mull.
**Physa fontinalis* Linn.
**Ancylastrum fluviatile* Mull.
**Planorbis contortus* Linn.
**Pisidium* sp. probably *P. lilljeborgii* Clessin

Crustacea

**Eurycercus* sp.
**Sida crystallina* (O. F. Müller)
Asellus meridianus Rac.
Gammarus pulex pulex (L)

Insecta

Ephemeroptera

Leptophlebia marginata Linn.
Caenis moësta Bengtsson

Plecoptera

Nemoura avicularis Morton
Capnia bifrons (Newman)
**Amphinemura sulcicollis* (Steph.)
**Perlodes microcephala* (Pict.)
**Isoperla grammatica* (Poda)
Diura bicaudata (Linn.)
**Protonemura meyeri* (Pict.)
**Chloroperla torrentium* (Pict.)

Hemiptera

Corixa dorsalis Leach
Corixa scotti (D and S)
**Micronecta poweri* (D and S)

Trichoptera

Limnephilus lunatus Curtis
L. rhombicus Linn.
L. flavicornis Fabr.
Potamophylax stellatus (Curtis)
Anabolia nervosa Curtis
Halesus digitatus Schrank
**Glyphotaelius pellucidus* Retzius
**Goëra pilosa* Fabr.
Lepidostoma hirtum Spence
Sericostoma personatum Spence
Tinodes waeneri Linn.
**Agapetus fuscipes* Curtis
Polycentropus flavomaculatus Pictet
Phryganea grandis Linn.
**Philopotamus* sp.

Mystacides nigra Linn.
Leptocerus sp. probably *L. aterrimus* Steph. Agrees with description by Lestage (in Rousseau 1921)

Neuroptera
Sialis lutaria Linn.

Coleoptera (larvae)
**Ilybius* sp.
**Agabus* sp.

Diptera
**Tipula* sp.
*Chironomidae larvae indet.

Teleostei
Cottus gobio Linn.
Coregonus clupeoides pennantii Cuvier and Valenciennes—eggs

(ii) *Surface and mid-water food*

Crustacea
**Bythotrephes longimanus* Leydig.

Insecta
Collembola
**Isotoma* sp.

Ephemeroptera
Leptophlebia marginata Linn. sub-imago and adult
Ephemera danica Mull. sub-imago and adult
Caenis mœsta Bengtsson. Adult

Plecoptera
Nemoura avicularis Morton Adult
Capnia bifrons (Newman) Adult
Taeniopteryx nebulosa (Linn.) Adult
Protonemura meyerii (Pictet) Adult
Plecoptera indet.

Trichoptera
Limnephilidae indet. Active pupa and adults
Trichoptera indet. Adults

Diptera
Chironomidae indet. Late pupa
Adult (aerial) Diptera

Adult (aerial) insects of terrestrial origin including Hymenoptera, Hemiptera, Diptera, Coleoptera

Mammalia
**Arvicola terrestris amphibium* L. (Water vole)

* Organisms marked with asterisks occur sporadically and in small numbers. They are of no importance as trout food and will be largely ignored in the rest of this paper.

Identification of Trichoptera larvae was greatly facilitated by reference to identified faunal collections prepared by Dunn (1952). Dr M. Pugh Thomas kindly identified specimens of *Eurycercus* sp. and *Sida crystallina*.

COMPOSITION OF THE DIET

An important point which deserves emphasis is that most trout move from the littoral to deeper water during the summer (Ball & Jones, 1961); since only trout in the littoral were available for this investigation, this implies that the summer diet of a large proportion of the trout is unknown, although it is most probable that they feed at the surface during this period, like the trout remaining in the littoral (see p. 605).

Table 1—Composition of the diet of Llyn Tegid trout. The percentage representation of each of the main food categories in the total food intake for the year. Assessed by the number, volume and occurrence methods. Based on 253 stomachs.

Food category	Percentage representation by		
	Number	Volume	Occurrence
Ephemeropteran nymphs	2·7	2·9	26
Plecopteran nymphs	2·3	1·6	21
Sialis lutaria larva	0·4	0·7	10
Trichoptera larvae	9·6	12·9	51
Chironomid larvae	0·2	+	2
Corixidae	0·2	0·4	5
Coleoptera larvae and adults	0·2	+	4
Asellus meridianus	5·3	4·3	20
Gammarus pulex	26·0	23·5	29
Mollusca	0·2	+	4
Ephemeroptera sub-imagines	2·2	5·2	8
Trichoptera pupae	0·7	2·5	4
Chironomid pupae	20·5	8·8	9
Terrestrial spiders	0·1	+	3
Cladocera	4·1	+	2
Aerial insects	20·0	23·2	36
Gwyniad eggs	5·1	1·7	8
Cottus gobio	0·1	12·1	4

The sign + indicates 0·1% or less.

Table 1 shows the percentage composition of the diet, assessed by the three methods applied. The results are based on stomachs taken throughout the year, and so refer to the total annual food intake. It can be seen that all three methods give essentially the same picture of the make-up of the diet. The volume method probably best expresses the relative nutritive importance of each food category, and the results obtained by this method will be taken as standard. The volume method is clearly unsatisfactory in one respect: it exaggerates the importance to the trout population as a whole of the large but relatively sparsely distributed *Cottus gobio*.

The number method (compared with the standard provided by the volume method) is unsatisfactory in two ways. It underestimates the relative importance of large animals, most noticeably *Cottus gobio*, but also Trichoptera larvae and pupae and Ephemeroptera sub-imagines (which were mainly the large *Ephemera danica*), and it overestimates the relative importance of very small organisms which were eaten in large numbers. This is most obvious in the case of chironomid pupae and Cladocera, and occurs less noticeably in the estimates of *Asellus*, *Gammarus* and gwyniad (*Coregonus*) eggs.

The occurrence method, as would be expected, greatly exaggerates the dietary importance of animals occurring in small numbers in many stomachs, an effect most clearly seen in the assessments of insect larvae and nymphs (Ephemeroptera, Plecoptera, Trichoptera), *Asellus meridianus* and aerial insects. This method is, however, quite strikingly successful in indicating the most important items in the general diet.

Table 1 shows that the trout is carnivorous with a wide variety of food animals. The few traces of vegetable material that were found in the stomachs were undoubtedly ingested incidentally with the animals with which they were associated. Out of eighty-eight animal species found by Dunn (1952) in the littoral fauna, forty were found in trout stomachs, plus three caddis larvae not collected by Dunn. The diet changes with season, so that very different pictures are given by stomach analyses made at different times of the year. Over the whole year, the most important single species consumed was *Gammarus pulex*, which made up 24 per cent by volume of the total food. Other important food animals were the caddis larvae *Limnephilus lunatus*, and *Potamophylax stellatus*, the Ephemeroptera *Ephemera danica* (especially the sub-imago) and *Leptophlebia marginata* nymphs, and *Asellus meridianus*.

Trout may feed on the lake bottom, in mid-water, or at the surface. Mid-water animals in Llyn Tegid include the plankton and swimming fishes, neither of which is of any importance in the trout diet. Only one stomach (in August) contained plankton (*Bythotrephes longimanus*), and the other cladocerans found, *Sida crystallina* and *Eurycercus* sp. are littoral forms, properly classified as bottom food (Pugh Thomas, personal communication). *Cottus gobio* (the bullhead) is a bottom-living fish which lurks in crevices between and under stones (Smyly, 1957). Bottom food made up 60 per cent by volume of the total intake (Table 1) and comprised insect nymphs and larvae, *Asellus*, *Gammarus*, the bullhead, and gwyniad eggs. Surface food (40 per cent by volume) included aerial insects, ephemeropteran sub-imagines, and pupae of chironomids and trichopterans. Animals in these last two categories could have been eaten as they ascended in mid-water to emerge at the surface, but most of the specimens found were on the point of emerging as adults and were always mixed with aerial insects, indicating that they were taken by the trout actually at the surface.

SEASONAL CHANGES IN THE DIET

1. *Surface feeding*

The monthly composition of the diet estimated by the volume method is presented in Table 2. The diet showed considerable seasonal variation,

Table 2—Percentage composition of the monthly food-intake, by volume.

	Dec	Jan	Feb	Mar	Apr	May	Jue	Jly/ Aug	Sep	Oct
No. of stomachs examined	34	29	10	60	29	13	28	11	19	20
Temporary bottom fauna										
Ephemeroptera nymphs	4·9	1·4	0·3	3·5	0·7	2·8	15·3	—	—	0·5
Plecoptera nymphs	0·6	0·9	2·2	6·8	4·7	0·1	0·5	—	—	—
Sialis lutaria larva	—	—	0·5	—	2·8	4·9	—	—	—	—
Trichoptera larvae	29·5	24·4	20·9	22·9	26·3	1·3	2·2	1·3	—	0·4
Chironomid larvae	—	—	+	—	—	—	—	—	—	—
Corixidae	—	—	—	—	—	—	—	—	3·9	—
Permanent bottom fauna										
Asellus meridianus	2·0	20·7	11·2	5·5	1·1	0·1	1·6	—	—	0·3
Gammarus pulex	58·0	46·0	13·9	40·4	4·0	2·9	1·5	—	—	68·5
Mollusca		0·1	—	+	—	—	+	—	—	+
Surface and mid-water food										
Ephemeroptera sub-imagines	—	—	—	—	—	—	52·1	—	—	—
Trichoptera pupae	—	—	—	—	—	—	24·5	—	—	—
Chironomid pupae	—	—	—	—	—	87·9	—	—	—	—
Aerial insects	5·0	4·0	0·7	0·7	34·7	+	2·3	59·3	96·1	30·1
Miscellaneous foods										
Gwyniad eggs	—	2·5	1·6	13·1	—	—	—	—	—	—
Cottus gobio	—	—	48·7	7·1	25·7	—	—	39·3	—	—
Cladocera	—	—	—	—	—	—	—	0·1	—	0·2
Surface and mid-water food	5·0	4·0	0·7	0·7	34·7	87·9	78·9	59·3	96·1	30·2
Bottom food	95·0	96·0	99·3	99·3	65·3	12·1	21·1	40·7	3·9	69·8

and the year can be divided into two main periods : October—April, when the trout fed predominantly on bottom-living animals, and May—September, when they fed mainly at the surface. Surface feeding also predominated in trout in Windermere and Malham Tarn from May to September (Allen, 1938 ; Holmes, 1960). In Llyn Tegid, this is the period during which the majority of the aquatic insects emerge as adults (Dunn, 1952) and includes the flight periods of most terrestrial insects, which suggests that the amount of surface feeding may be largely controlled by the amount of available surface food. Allen (1938) arrived at the same conclusion for Windermere trout, and pointed out that in one year when good weather caused adult insects to be available early from April onwards, the trout food also contained large numbers of aerial insects from April, whereas in another year, insect emergence being delayed by bad

weather, surface feeding did not become frequent until mid-June. This illustrates the opportunism which characterizes the feeding of brown trout as well as that of salmon parr, of which Carpenter (1940) wrote : " every food organism is taken in highest numbers at its season of best availability ".

The greatest consumption of surface food was in September, when 90 per cent of the total consisted of adult insects, mainly Diptera, Hymenoptera and Hemiptera of terrestrial origins. In October, bottom food predominated (70 per cent), and surface food consisted of adult Diptera, Hymenoptera and Trichoptera. During the winter, the small amount of surface food (5 per cent or less) was composed entirely of small adult Diptera of terrestrial origin, reinforced in March by a few individuals of the early-flying stone-flies *Capnia bifrons* and *Taeniopteryx nebulosa* and in April by adult *Nemoura avicularis* and *Protonemura mayeri* and large numbers of adult Chironomidae. In May, surface food (88 per cent) consisted mainly of small newly-emerged chironomids (chironomid pupae in the table), with wings still crumpled, which must have been taken while resting on the surface before flying away. The June surface food (79 per cent) consisted mainly of Ephemeroptera sub-imagines (mainly *Ephemera danica* with some *Leptophlebia marginata*) and swimming caddis pupae (*Limnephilus lunatus* and several species undetermined). Aerial insects were also taken, and included adult Trichoptera, Diptera, Ephemeroptera, (*E. danica* and *Caenis moësta*) and Plecoptera (*N. avicularis*). Surface food in July and August (59 per cent) consisted of adult insects of terrestrial origin (Diptera, Hymenoptera and Hemiptera), and in one stomach about 600 adult *Caenis moësta*.

Thus, surface food was taken all the year round, was unimportant in the winter (December—March) and predominated during the summer (May—September). It comprised a wide variety of aerial insects, with an important element of insects of terrestrial origin, and in May and June included pupae or sub-imagines of Chironomidae, Trichoptera and Ephemeroptera.

2. *Bottom feeding*

Humphries (1936) appears to have been the first to make a formal distinction between the permanent bottom fauna of a lake (e.g. *Gammarus*, *Asellus*, molluscs, hydracarines) and the temporary bottom fauna, animals which spend only part of their life cycle in the lake (insect larvae and nymphs). Allen (1938), in considering the bottom fauna as a source of fish food, pointed out that the bottom fauna is available throughout the year, which was confirmed by Dunn (1952), but that the temporary bottom fauna, though present in the winter, is then composed of small-sized individuals and only becomes suitable for fish-food in spring when individuals have grown larger. Temporary forms will also be scarce in the summer, because of the emergence of adult insects (Dunn, 1952). Reduced activity in the winter due to low temperatures, and migration to shallow water prior to emergence in spring are other factors which will affect the availability of some or all of the members of the temporary bottom fauna. Allen (1938) showed that the representation of the two groups of bottom animals in the stomachs of Windermere trout followed this pattern

of availabilities, molluscs and crustaceans predominating in October—February, and insect nymphs and larvae in March to July.

The permanent bottom fauna of Llyn Tegid contributes mainly *Gammarus pulex* and *Asellus meridianus* to the trout diet (Table 1, and pp. 613–614). In Table 3, the percentage of the total invertebrate bottom fauna eaten which is temporary (insect nymphs and larvae) is given for each month. As in Windermere, insect nymphs and larvae showed a spring predominance over the permanent bottom fauna, probably the result of the great increase in size of the insects at this time of year as Allen (1938) concluded. Greater individual activity due to higher temperature, emergence, and in some cases migration to shallow waters, are other factors which may have caused the increased consumption of insects at this time ; these matters are referred to again below, pp. 609–615.

Table 3—Percentage of insect young stages (temporary bottom fauna) in the total invertebrate bottom fauna consumed.

	Dec	Jan	Feb	Mar	Apr	May	Jue	July/Aug	Sep	Oct
By number	45	28	32	33	76	67	73	100	100	15
By volume	37	29	49	42	87	75	86	100	100	14

The total dominance of temporary forms in the bottom food in July, August and September requires comment. The absence of *Gammarus* and *Asellus* in the food at this time could not be due to their scarcity since Dunn (1952) found these animals to be more abundant in summer than in the winter when they were important food items. Aerial insects predominated in the diet at this time (Table 2), and the absence of the Crustacea may simply reflect the small number of stomachs examined that contained bottom food (eight in the period July to September). Larger samples might reveal that some of the few fish feeding on the bottom at this time did eat *Gammarus* and *Asellus*.

In October, *Gammarus* again predominated and the temporary bottom fauna taken at this time was composed mainly of *Limnephilus lunatus* larvae, with a few *Ephemera danica* nymphs. From December to March, *Gammarus* and *Asellus* formed the main food, followed in April, May and June by the spring dominance of insect larvae and nymphs. Of the temporary bottom forms taken in winter, Trichoptera (mainly *L. lunatus* and *Potamophylax stellatus*) were the most important.

The utilisation of some of the animal groups as food by the trout is considered in another section. Considering the utilisation of the fauna as a whole, it would appear that trout prefer surface food to the permanent bottom fauna, since *Gammarus* and *Asellus* are even more abundant in summer, when surface feeding predominated, than in winter when they formed an important part of the diet. Furthermore, the importance of surface feeding in April, May and June, when the littoral temporary bottom fauna is more abundant and composed of larger individuals than in winter (Dunn 1952) suggests that surface food is also preferred to the temporary bottom fauna. Thus, it seems that when both surface and bottom foods are available, trout prefer to feed at the

surface rather than at the bottom. However, trout have an annual cycle of physical activity, probably related to daylength, temperature, and thyroid activity, (Swift, 1955, 1959), and display less physical activity in winter than in summer, when the choice between surface and bottom feeding is offered. Surface feeding must involve more activity than feeding on the lake bottom, and it is quite possible that if offered abundant surface food in winter the trout literally would not have the energy to make use of it.

The spring predominance of insects in the bottom food led Allen (1938) to conclude that trout will feed on the temporary bottom fauna rather than on the permanent bottom fauna, implying that they actually select insect nymphs and larvae in preference to *Gammarus* and *Asellus*. This conclusion is probably invalid, since Dunn (1952) has shown that the faunal density of insects in the shallows of Llyn Tegid in spring greatly exceeds that of *Gammarus* and *Asellus* combined. The increased activity of the insects prior to emergence and pupation will further enhance their availability. During winter, Dunn recorded densities of insect larvae and nymphs much lower than in spring ; *Limnephilus lunatus*, for example, one of the main insect foods, was nearly three times as abundant as *Gammarus* in spring, but occurred at about the same density as *Gammarus* during the winter, when its small size and reduced activity would make it still less available than in spring. It seems reasonable to conclude that the proportion of temporary and permanent bottom animals eaten by the trout is decided by the relative availabilities of the two groups, and not by preferential selection by the fish.

3. *Seasonal variations in the quantity of food eaten*

Seasonal changes in the amount of food eaten by the trout have been investigated by calculating for each month the mean volume of food in the stomachs containing food (i.e. excluding the completely empty stomachs). The results are shown graphically in Fig. 1 together with the fullness index. The June sample has been omitted, since it consisted only of small fish (less than 200 mm. length), but in all other months the stomachs were taken from fish covering the size-range 100–330 mm. length, so the mean volume of food per stomach can be compared from month to month as an index of the amount of food eaten.

The mean volume of food in the stomachs varied seasonally, with a maximum in summer about eight times the winter level. Since digestion will proceed more rapidly at summer temperatures then in winter (Hewitt, 1943), the summer food intake must in fact have been more than eight times the winter rate. Hathaway (1927), working with coarse fish, found that the amount of food eaten by the same individuals at 20°C was about three times that at 10°C, and Brown (1946 c) found that the food intake of the two-year-old brown trout increased gradually with temperature from 4·5°C to about 19°C and fell sharply at higher temperatures. In the lake, in addition, in spring and early summer, (March to June), the total quantity of food available to the fish is greater than in the winter (Dunn, 1952 ; see previous section). Food intake was rather less in late summer and autumn than in early summer, but still was greater than in December to February.

Changes in the monthly fullness index (Fig. 1) again indicated a greater rate of feeding in summer than in winter, and agreed well with the results for the mean volume of food eaten.

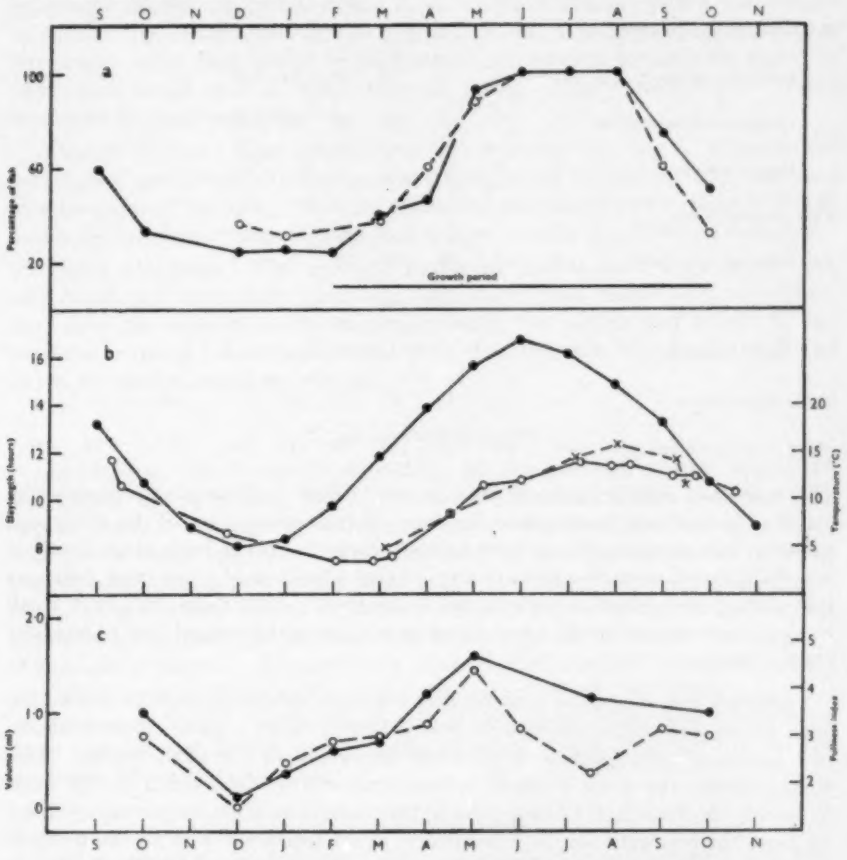

Fig. 1 a—Growth. Percentage of trout with open-margin scales : 1952–53 results O- - - - - -O, 1953–54 results ●———● (from Ball & Jones, 1960).
b. Physical factors. Daylength ●———● and temperature at 1 metre depth : 1952–53 results x- - - - - -x and 1953–54 results O———O.
c. Rate of feeding. Mean volume of food per stomach ●———● and the monthly fullness index O- - - - - -O.
Daylength derived from the sunrise and sunset figures for Birmingham given in Whitaker's Almanac. Birmingham lies at about the same latitude as Llyn Tegid.

NOTES ON THE UTILIZATION OF SOME FOOD ANIMALS

1. *Ephemeroptera nymphs*

Three species were found in the stomachs (Table 4).

Ephemera danica is a burrower in mud or grit (Dunn, 1952), so is not readily available as food to the trout which is a superficial feeder (section 4 below).

Table 4—Occurrence of some insect nymphs and larvae found each month, expressed as number per 100 stomachs.

	Dec	Jan	Feb	Mar	Apr	May	Jne	Jly/Aug	Sep	Oct
Ephemeroptera nymphs										
Ephemera danica	21	17	—	22	10	54	250	—	—	40
Leptophlebia marginata	—	10	20	222	62	46	121	—	—	—
Caenis moësta	6	3	—	—	—	—	—	—	—	—
Plecoptera nymphs										
Nemoura avicularis	3	17	60	148	241	—	6	—	—	—
Capnia bifrons	—	—	30	103	30	—	—	—	—	—
Diura bicaudata	—	—	—	12	—	—	—	—	—	—
Sialis lutaria larva	—	—	10	—	103	154	—	—	—	—
Number of stomachs	34	29	10	60	29	13	28	11	19	20

The increased consumption of this species in May to June was probably the result of individuals leaving their burrows prior to emergence, all the specimens found at this time being large with big wing-buds. Also in June, large numbers of sub-imagines were found in the stomachs, which must have been taken as they rested on the surface prior to the final moult. After June, only very small nymphs are present in the lake, which grow during the second half of summer (Dunn, 1952).

Leptophlebia marginata is essentially a littoral swimming nymph associated with rooted vegetation (Mellanby, 1951 ; Dunn, 1952). Dunn found evidence of a shoreward migration in April when emergence of the adult begins. This would explain the great increase in the number of nymphs eaten by the trout in March, the drop in April being due to the emergence of the migrating nymphs. In June the consumption of *Leptophlebia* again increased, and all the nymphs found in the stomachs were very large and on the point of moulting to produce the sub-imago. Possibly there is a second shoreward migration in June, or else an increase in the activity of nymphs already present in the shallows. Large numbers of the sub-imagines were found in June, and some adults. During July to February, the nymphs are probably too small and sheltered by weed to be eaten in quantity by trout.

Caenis moësta. Only three specimens were found. Dunn records this species as occurring all round the lake, and abundant at one of the regular netting stations where mud and rooted plants abound. The nymphs are dull-coloured, slow-moving and generally carry mud and epiphytes on their backs. As Frost (1939) has suggested, this camouflage probably protects them from predation. Adults were found in stomachs in June and July, one fish in June containing about 600.

2. *Plecoptera nymphs*

Nemoura avicularis is the commonest stone-fly in the lake. Dunn found a maximum density in January, and some adults in March, with a main flight in April. The consumption of the nymphs by trout was heaviest at the time of emergence, when they would be most active and moving towards the shore for their final moult out of water (Hynes, 1941). Adults were found in the stomachs in April and June.

Capnia bifrons. This species was not recorded by Dunn, although its presence in quantity in trout stomachs suggests that it must be fairly common in some parts of the lake. Many nymphs and some adults were taken in March again the maximum consumption was of late nymphs just before emergence.

Diura bicaudata. The nymphs found in March were very large with well-developed wing-buds, probably near their final moult. Hynes (1941) says that the nymphs move to deeper water for winter and return to the shallows in spring before emergence, which would explain why none were found in the stomachs during the winter.

3. *Sialis lutaria larvae*

Apart from one found in February, all the specimens were full-grown and taken in April and May. Dunn (1952) recorded the species at all depths down to 20 metres, but it was rather scarce in the littoral. When fully-grown the larvae quit the water and pupate near the edge, in soil or reeds. Pupation lasts about three weeks and the flight period is May to June (Kimmins, 1944). Dunn found adults in these months at Llyn Tegid. Doubtless the, advanced larvae eaten by the trout were migrating individuals on their way out of the lake to pupate. Their absence from the diet at other times is explained by their burrowing habit and by their relative scarcity in the littoral.

Frost and Smyly (1952) found large numbers of *Sialis lutaria* larvae in trout stomachs in March in the Lake District, again probably due to the migration of the mature larvae.

4. *Trichoptera larvae*

Caddis larvae are an important food, especially during December to April. Fourteen of the fifteen species listed by Dunn were found in the stomach content (Table 5), together with three species not recorded by her, *Phryganea grandis*, *Leptocerus aterrimus*, and *Philopotamus* sp. Most important as food was *Limnephilus lunatus*, the second most abundant caddis in the lake. The most abundant species, *Tinodes waeneri*, was hardly ever eaten by trout (see below). Dunn found *L. lunatus* pupae in the fauna in May and June, and active (swimming) pupae occurred in the trout stomachs in June (Table 2). The maximum consumpton of larvae was just before pupation, in April (Table 6), the month in which Dunn recorded a maximum population density, and when the larvae are largest and most active. *Halesus digitatus* and *Sericostoma personatum* were also eaten most in the months in which Dunn recorded maximal densities, and *Anabolia nervosa* was eaten most in February, the maximum being in March. Unfortunately, Dunn did not give density

Table 5—Mean number of larval Trichoptera per 100 stomachs.

	Dec	Jan	Feb	Mar	Apr	May	Jue	Jly/ Aug	Sep	Oct
Limnephilus lunatus	56	250	140	485	775	38	3	—	—	20
L. rhombicus	9	17	—	10	—	—	—	—	—	—
L. flavicornis	12	20	120	44	—	—	—	—	—	—
Potamophylax stellatus	127	225	310	49	54	—	—	—	—	—
Anabolia nervosa	—	35	70	35	14	—	—	—	—	—
Halesus digitatus	3	4	—	10	142	—	—	—	—	—
Glyphotaelius pellucidus	6	—	—	—	—	—	—	—	—	—
Goëra pilosa	12	4	—	—	—	—	—	—	—	—
Sericostoma personatum	—	49	—	25	38	—	7	—	—	5
Lepidostoma hirtum	—	4	—	25	38	—	7	—	—	5
Tinodes waeneri	—	4	—	—	4	—	—	—	—	—
Agapetus fuscipes	—	4	—	2	—	—	—	—	—	5
Polycentropus flavomaculatus	6	10	20	4	10	—	—	—	—	—
Phryganea grandis	—	14	—	7	20	—	—	—	—	—
Philopotamus sp.	—	4	—	—	—	—	—	—	—	—
Mystacides nigra	9	—	—	3	7	—	17	—	—	—
Leptocerus aterrimus	3	—	—	—	—	38	50	92	—	5
No. of stomachs	34	29	10	60	29	13	28	11	19	20

record for *Potamophylax stellatus*, the second most important caddis in the diet, and did not record *Leptocerus aterrimus* which is eaten during summer. According to Morgan (1956), in Scottish lochs as in Llyn Tegid, large numbers of larval *L. aterrimus* are eaten by trout from May to July, and Morgan showed that this is due to their migration inshore to pupate on the shoreline when the larvae are at their largest and most active. The same explanation probably holds for Llyn Tegid, and for the heavy May consumption of this species in Three Dubs Tarn (Frost & Smyly, 1952). Thus, changes in the consumption of the caddis larvae can be explained by reference to their abundance and behaviour.

Caddis pupae, which were eaten in June, were always active swimming forms as in Loch Moraig trout (Morgan, 1956). These will be readily available to the trout for a short time as they swim to the surface after quitting the pupae case. Neill (1938) commented on the extreme vulnerability of ascending caddis pupae. The pupae are not, however, eaten when stationary in the case, an illustration of a characteristic of trout feeding behaviour which can readily be observed in aquaria : they take only moving food, and show no interest in completely stationary (but otherwise suitable) material (see too, Brown, 1951 ; Stuart, 1953).

Comparison of the caddis larvae eaten by the trout with those found in the stomachs of grayling (*Thymallus thymallus* L.) in Llyn Tegid suggests a marked difference in the feeding habits of the two species (Table 6). *Polycentropus flavomaculatus* and *Agraylea multipunctata* were the two caddis larvae eaten most frequently by the grayling, whereas they are rarely or never taken by trout. Both grayling and trout were caught together in the regular nettings, and presumably were using the same feeding grounds. The differences in the

Table 6—Numbers of larval Trichoptera species eaten by grayling and trout in the period January–June, expressed as numbers per 100 stomachs.

	Grayling (24 stomachs)	Trout (109 stomachs)
Limnephilus lunatus	54	300
L. rhombicus	—	5
L. flavicornis	—	17
Potamophylax stellatus	—	102
Anabolia nervosa	—	20
Halesus digitatus	—	39
Goëra pilosa	—	1
Sericostoma personatum	8	20
Lepidostoma hirtum	59	13
Tinodes waeneri	59	2
Agapetus fuscipes	—	1
Polycentropus flavomaculatus	430	8
Phryganea grandis	—	10
Philopotamus sp.	—	1
Mystacides nigra	—	3
Leptocerus aterrimus	21	20
Agraylea multipunctata	75	—

caddis diet therefore was probably due to differences in feeding behaviour. Some idea of these differences comes from considering the habits of the caddis larvae. Of those favoured by grayling, *Polycentropus flavomaculatus* larva lives on the undersides of stones, where it constructs a pocket-shaped net with a terminal retreat or home. *Tinodes waeneri* has similar habits, but constructs tortuous tunnels on the surface of the stones in which it lives. *Agraylea multipunctata* larvae are very small and live in clusters, their cases fastened beneath stones (Lestage in Rousseau, 1921 ; Hickin, 1950, 1952 ; Dunn, 1952). In contrast, the caddises most commonly eaten by trout, *Limnephilus lunatus* and *Potamophylax stellatus* are large and move freely amongst plants and stones. Thus, it appears that trout are more superficial feeders than grayling, eating the more obvious and readily accessible larvae. Neill (1938) has remarked " the trout does not normally follow the habit of rooting in the substratum to the extent of carp and other bottom feeding fish ", and the shape of the grayling's mouth seems better adapted to rooting amongst stones and plants than that of trout. The grayling in Llyn Tegid had eaten many more molluscs than trout, again suggesting a rooting habit ; and in rivers, too, the two fishes feed differently, the trout having a resting position in quiet water from which it launches out at moving food, and to which it immediately returns, the grayling, in contrast, lying in mid-stream and taking food directly from stones or plants on the stream bed, eating even Helmid beetles from concealed habitats and attached molluscs (Fabricius, 1953 ; Müller, 1954 ; Kallenberg, 1958). As in streams, it is probable that in Llyn Tegid these feeding differences virtually eliminate feeding competition between grayling and trout.

5. *Molluscs and corixids*

Molluscs are of little importance to Llyn Tegid trout, in contrast to trout in the Lake District (Allen, 1938 ; Swynnerton & Worthington, 1940 ; Frost

& Smyly, 1952). The reasons for this are not clear. *Limnea pereger*, *Physa fontinalis*, *Ancylastrum fluviatile* and *Pisidium lilljeborgii* are abundant in the lake according to Dunn, but few individuals were found in the trout stomachs. All the gastropods in Llyn Tegid are poorly-developed specimens, invariably small with thin shells, (Dunn, 1952), several species averaging only half the size quoted as typical by Macan (1949). Possibly their small size and slow movement may lead to neglect of the molluscs by the trout.

Of the corixids, *Micronecta poweri* occurs abundantly in the littoral but was hardly ever found in the stomachs. *Corixa dorsalis* and *C. scotti* were found in small numbers in the stomachs only in September. These bugs are plentiful in weed beds in the lake (Dunn, 1952), and it is possible that they are not eaten to any extent by the trout because they secrete substances distasteful to fish (Frost & Macan, 1948). That fish hardly ever eat corixids is a rule of wide-spread application (Frost & Macan, op. cit.), but is not universally true. Mr C. Myers has kindly shown me his records of trout stomach contents from Blagdon Lake, in which corixids (probably *C. dorsalis*) formed the main food during daytime in June to December, and were commonly eaten in October. Again, Phillips, (1929) records Corixidae as an important trout food in New Zealand.

6. *Fish*

Allen (1938) found that a few trout of all sizes in Windermere had eaten very small fish, usually minnows, less than 50 mm. in length. There was also a tendency for large trout (over 400 mm.) to feed on other fish, usually 100–150 mm. in length. In Haweswater, (Swynnerton & Worthington, 1940) fish (sticklebacks, and probably minnows) were important food only for the large trout (250–350 mm.).

In the present investigation, only five out of the 253 stomachs examined contained fish, or traces of fish, in each case the bullhead, *Cottus gobio*. The sizes of these piscivorous trout ranged from 150 mm. to 310 mm. in length. It appears that the bullhead (length 20–40 mm.) is eaten by quite small trout in Llyn Tegid, corresponding to the consumption of very small fish by trout of all sizes in Windermere. The bullhead lurks on the lake bottom or under stones (Smyly, 1957) and individuals are probably eaten by trout in the course of their feeding on bottom-living invertebrates.

It cannot be said whether larger trout, 400 mm. and over, are predominantly piscivorous as in Windermere, stomachs from such fish not being available. The largest trout examined for food was 385 mm. long and caught in January. The stomach contained a few mammalian tail vertebrae with hairs, identified as *Arvicola terrestris amphibium* (the water-vole) by Dr T. C. S. Morrison-Scott of the British Museum, (Natural History).

Gwyniad eggs

The gwyniad (*Coregonus clupeoides pennantii*) spawns on the rocky shore in the shallowest water in January to February. The eggs have been found scattered in groups between small boulders and stones, readily accessible to trout. During January to March, large numbers of gwyniad eggs were found in

trout stomachs (Table 2). Allen (1938) found that trout in Windermere similarly ate the eggs of the charr (*Salvelinus*), which spawns in the Windermere shallows in November. In March, many of the gwyniad eggs in the stomachs were eyed. None was eaten later than March, which suggests that the young gwyniad must hatch at the end of March or beginning of April, the young being in some way protected from being eaten by trout. A single gwyniad alevin hatched and kept in the laboratory was extremely and continuously active and appeared to prefer light to darkness when given the choice (Hughes, personal communication), which suggests that in nature the young gwyniad might be pelagic, perhaps in deep water as Slack (1952) suggests for the closely related powan, *Coregonus clupeoides*.

FOOD IN RELATION TO SIZE

Allen (1935) established well-marked changes in diet with increasing size in the perch, and emphasized the necessity of such changes (usually involving the consumption of larger and larger organisms) if the fish is to obtain the increasing volume of food it needs as it grows. In Windermere the same worker (Allen, 1938) found that all the trout he examined had much the same diet (bottom-living invertebrates) except for the few fish over 400 mm. in length which fed mainly on fish. A similar change-over to fish-eating by larger trout was reported in Haweswater by Swynnerton & Worthington (1940), in the River Liffey by Frost (1939) and in Swedish lakes by Nilsson (1955). An increased consumption of molluscs with size and age has also been reported (Swynnerton & Worthington, op. cit. ; Allen, 1951 ; Nilsson, op. cit.).

In Llyn Tegid, molluscs were of no importance as trout food, and no really large (and probably piscivorous) individuals were examined. A comparison of the food of large and small trout has been made, and the details reported elswhere (Ball, 1957). It showed that within the size and age range concerned (88–344 mm. length, ages 0+ to IV+) there was no major change in diet. During the winter, there was a slight tendency for fish over 200 mm. to eat relatively more *Gammarus* and *Asellus*, and fewer insect nymphs and larvae, and in summer very small trout (under 140 mm.) took less surface food than larger individuals ; but all the trout examined were in the insect-feeding stage.

DISCUSSION

It is clear from the present results that the trout is fairly described as an opportune carnivore, taking whatever food animal is most accessible and exercising little or no selection ; the possibility of avoidance of corixids because of their distasteful qualities has been noted. The same conclusion was reached by Pentelow (1932), Neill (1938), Butcher (1945), and Nilsson (1955). Allen (1938) concluded that seasonal changes in the diet could be explained by changes in the availability of the fauna, but thought nevertheless that individuals tended to select food organisms, since he found trout which contained more than 60 per cent by number of a single food animal. Arguing that it is unlikely that any one species will make up 60 per cent of the fauna, he interpreted this as evidence of selection. However, patchy concentrations of single species may occur, and in addition to their numerical proportion in the fauna,

the size and habits of food organisms must greatly influence the relative extent to which they are eaten. Allen's criterion of selection seems too arbitary to make his demonstration of active food-selection convincing. Like the salmon parr studied by Carpenter (1940), and within the limits imposed by the size and habits of the food animals, the trout is indiscriminately carnivorous. The most important animals eaten are those which are most readily accessible in the fauna.

Concerning the reasons for the seasonal changes in the diet enough has already been said to indicate that the proportions of the different food organisms consumed probably depends on their relative availabilities. However, the determination of the total quantity of food consumed probably lies to a great extent in physiological changes in the trout, in their turn controlled ultimately by environmental seasonal variables, such as temperature and daylength. The nature of the environmental control of seasonal changes in salmonids has attracted considerable attention (see e.g. Allen 1940, 1941 b ; Wingfield, 1940 ; Brown, 1946, a, b, c ; Swift, 1955), and little can here be added to these discussions except to draw attention to the relationship between the annual feeding cycle and daylength changes. (Fig. 1).

The improved growth commonly shown by trout introduced into waters with a better food supply but with no change in the major physico-chemical conditions suggests that food supply can limit food intake in nature, at least at some times of the year, probably in spring and summer when most growth occurs. However, it is unlikely that food intake is limited by food supply at all times ; for example, during September to March, the decline and rise in food intake (Fig. 1) is not paralleled by changes in food supply (Dunn, 1952). From December to March, the main food animals are *Gammarus pulex*, *Asellus meridianus* and caddis larvae, none of which increases in size, activity or abundance at the low and declining temperatures of this period ; but the food intake increases steadily from December onwards, parallel to the daylength cycle. Increasing daylength rather than temperature or food supply, appears to induce the winter increase in food consumption. From the end of March onwards, the temperature rises, and the food animals increase in size, physical activity and, in some cases, abundance (Dunn, 1952). Rising temperature too, directly increases the appetite of trout up to 19°C (Brown, 1946 c), so that increasing daylength, temperature, appetite and food supply are probably all concerned in the rise in food intake from March to May, probably with the food supply as the limiting factor.

The drop in the volume of food after May–June may be partly an artefact due to the increased digestive rate at the higher summer temperature (Hewitt, 1943). However, rising temperature also increases the appetite, leading to greater food intake if supply is sufficient (Hathaway, 1927 ; Brown, 1946 c). This latter worker experimentally showed that trout food consumption increase up to 19°C, so it is not likely that food intake was being limited after June by high temperature, which reached a peak of only 16°C in August–September. The food consisted almost entirely of surface forms in July to September, and these are on the average smaller and perhaps more sporadically encountered

than the bottom-dwelling animals which predominated in the diet in March to June. This could result in an effective decrease in food-supply, which would account for the lowered food-intake in July–September compared with March–June.

The drop in feeding from October to December is associated with falling temperature and decreasing daylength. The availability of the bottom fauna may decline to some extent, as their activity will decrease with temperature, but it does not seem likely that this alone could cause such a marked decline in food intake. Probably physical factors are again limiting ; Fig. 1 suggests that daylength may be the primary control, as in December to March.

This suggested model of the seasonal cycle in feeding, then, involves daylength as an important environmental control of food intake, with temperature reinforcing the effects of daylength when the two factors run parallel (October to December, March to May), but being over-ridden when daylength is increasing with decreasing temperature (December to March). Superimposed on this physical control, the food intake is probably limited by food supply in the latter part of summer (July to September) and in spring (April to May).

The mode of action of the physical factors needs investigation. Being predominantly visual feeders, trout will tend to eat more when given longer days for the detection and capture of food. It is altogether, likely, though, that the endocrine system acts as mediator between environmental changes and the physiological alterations which are expressed in the seasonal cycle. Temperature and illumination changes are known to alter pituitary activity in teleosts (Hoar, 1957 ; Pickford & Atz, 1957) and Swift (1955) has demonstrated in adult trout a seasonal cycle in thryoid activity correlated with the daylength cycle, and probably mediated via anterior pituitary thyrotrophin (Pickford & Atz, 1957). The thyroid hormone increases physical activity in salmonids (Hoar *et al.*, 1955 ; Swift, 1955) and regulates general metabolism in fishes (Hoar, 1957 ; Pickford & Atz, 1957 ; Hopper, 1959). Furthermore, when hypophysectomised *Fundulus* were injected with pituitary growth hormone one of the first effects was an obvious increase in appetite (Pickford & Atz, 1957), indicating the possibility that stimulation of the trout pituitary growth hormone output by increased daylength and temperature may directly increase the appetite, in addition to the more indirect effect via thyrotrophin, thyroid hormone and general metabolism.

It is interesting to note that the seasonal growth pattern of trout in Llyn Tegid is more closely correlated with the daylength cycle than with temperature changes (Ball, 1957 ; Ball & Jones, 1960 ; Fig. 1). Again, the obvious interpretation is that the pituitary output of growth hormone and thyrotrophin is altered by changes in daylength and temperature, daylength being the primary control, and that the effects of growth hormone and thyroid hormone on metabolism provide the internal determination of the growth cycle ; but extensive experimental information is required to establish this explanation.

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TAXONOMIC REALISM

BY

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In ornithology, check lists are still always arranged in what purports to be a " natural " order of species and genera. Such a system has inescapable weaknesses and the results are delusive and misleading. It is recommended that within the genus the species should, so far as possible, be allocated to numbered species-groups (reasons to be published by the reviser), that the specific names should be printed in alphabetical order, and that each should have suffixed to it the number of any species-group to which it belongs. The use of alphabetical order has come increasingly into favour in other branches of zoology.

The earliest lists of animals tended to be in alphabetical order, so that the most diverse animals very often found themselves in juxtaposition. In reasonable reaction to this, and largely in consequence of the Linnaean classification, it became the rule to place together those species which appeared to be most closely related ; and eventually the taxa at all levels were thus arranged. Now however, especially with the enormous increase in the number of species known, the operation of this system meets with increasing difficulties and objections.

This subject was recently forced on my attention by the fact that I was asked to contribute to the concluding volumes of a check-list of the birds of the world. The pattern, established in earlier volumes, the first of which appeared thirty years ago, was the familiar one, common to probably all ornithological lists, of a supposed approximation to a " natural " sequence. The idea was that the components of each taxonomic category were arranged with the most " primitive " first, and that the names of those taxa which appeared to be most closely related were printed in juxtaposition. Whatever its merits, this system faces the insuperable objection, which has of recent years frequently found explicit recognition, that a linear arrangement cannot adequately represent an evolutionary system that is more than two-dimensional. In any case, within the genus anyone seeking to construct a linear " natural " arrangement must have in mind an idea of species-groups, whether designated subgenera or more vague and informal ; and if he carries out his system faithfully, he must come to conclusions on the sequence within each species-group, on the sequence of the species-groups among themselves, and on the points in the list at which he shall insert any species that he cannot conscientiously allocate to a species-group. The unallocated species include not only those which are transitional between two groups but also peculiar members of the genus. Irrespective of whether enough is known of both the life history and the morphology of the various taxa to justify these efforts, the result will be a list in which, while the most closely related species are indeed in juxtaposition, so also, repeatedly, are those which are not particularly closely related, and the list, as conventionally prepared, gives no clue whatever to the points of

discontinuity in the arrangement. Consider one of the simplest examples, a genus of four species, of which two are particularly close, and so form a species-group. In whatever order the four are arranged, there will be two points (in no way indicated) where unlike species are in juxtaposition, against one point in which proximity is justified. As for the sort of thing that has actually been going on in taxonomic arrangements for many years, I may cite the case of an avian genus of nine species, the latest two workers on which have put the species in different sequences, without either of them publishing an explanation or justification of what he has done. One of these writes privately ; " I shall have to confess that I have no good reason to argue for any particular sequence of species within the genus ".

I have been especially concerned with the Ploceidae, the weaver-bird family. It includes one large group, *Ploceus sensu lato*, containing about sixty species. Many diverse methods of breaking this group into genera and subgenera have been proposed, with differing sequences of these taxa and of their constituent species. As seems very generally to be the case, the merits of most of these arrangements have not been argued in the literature by their respective proponents and there is nothing, not even the sanction of tradition, to suggest that any particular one of them ought to be followed rather than another. An additional difficulty is that, though it could plausibly (but not conclusively) be argued that one of the species-groups is the most " primitive " and so entitled to be placed first, it seems to me impossible to arrange the great majority of the species or groups of species in any order that has any " natural " justification. In fact I had to abandon the attempt. And it is worth while to emphasize that this is a group in which for some species an unusually wide variety of characters can be used, not only of plumage (often brilliant), bodily proportions and characters of eggs, but also of nest architecture and details of behaviour.

The alternative I adopted was first to decide what informal species-groups could be suggested, and to give each a number. These groups between them accommodated fifty species out of the fifty-seven. In the final list the whole of the species were arranged in alphabetical order, and those which belong to the same species-groups had the appropriate reference number inserted after them in brackets. A species showing characters of two groups, which under the usual convention would be forced into one of them or treated as a monotypic subgenus or species-group, was designated by both appropriate species-group numbers, in the form $3 \geqslant 4$, for example. Aberrant species, not attachable to any group, bore no number. This system seemed to me to give as much information as possible of relationships within the genus, without ambiguities, without rigidity and with less element of that fiction which must enter to some extent into any attempt at achieving a " natural " sequence in linear form. As a simple illustration I may quote the genus *Euplectes sensu lato*, which includes the bishop birds and the whydahs. On the left appears the alphabetical sequence, amplified as I recommended, and on the right the " natural order " of a previous worker on the group, with whose opinions I largely agree. Museum collections could of course, if desired, be arranged by the species-groups (and alphabetically within them).

Species-group (1) *hordeaceus*	
(2) *macrourus*	
Euplectes	
afer (1)	*Euplectes*
albonotatus (2)	*orix*
ardens (2)	*nigroventris*
aureus (1)	*hordeaceus*
axillaris (1 2)	*gierowii*
capensis (1 2)	*afer*
diadematus (1)	*diadematus*
gierowii (1)	*aureus*
hartlaubii (2)	*capensis*
hordeaceus (1)	*axillaris*
jacksoni	*albonotatus*
macrourus (2)	*macrourus*
nigroventris (1)	*ardens*
orix (1)	*hartlaubi*
progne (2)	*jacksoni*
	progne

It seems possible that the weight of ornithological conservatism, which is such that all modern check-lists of birds have been attempts at " natural " arrangement, will preclude the adoption of the more realistic system here advocated for the weaver-birds. Hence it has seemed to me worth while to ascertain what systems have been followed in the recent check-lists of other branches of zoology. In order to obtain a random sample I approached individual specialists in Oxford and in the British Museum (Natural History) and asked them to show me one or two of the lists, prepared in the last twenty years or so, which are in standard use. Thanks to their co-operation, which I gratefully acknowledge, the following can be regarded as reflecting modern taxonomic practice in this respect.

Invertebrate marine organisms. In " Plymouth Marine Fauna " 1957 (Marine Biological Association), which deals with a large number of groups, " the classification adopted is mainly one of convenience and does not conform with any other ". In fact, in a few groups, e.g. the Foraminifera and some genera of the Ceratinomorpha the species are arranged alphabetically, and in a small number of others, e.g. some in the Portunidae, they are arranged by date of publication, but the arrangement in the great majority of the groups is not self-explanatory and is presumably " natural ".

Parasitic worms. In the " Cestodes of France ", Joyeux & Baer (1936), the species are arranged alphabetically, while in Dawes' (1947) " Trematoda of British fishes " they are not.

Araneae (*Spiders*) " Katalog der Araneae ", Roewer, 1942, has both genera and species arranged alphabetically.

Insects. In " British insects ", Kloet & Hincks, 1945, the arrangement of species in a small minority of genera is alphabetical but in the others it does not explain itself.

Lepidoptera. Peters' " Butterflies of the Ethiopian Region ", 1952, is in unexplained order.

Coleoptera. Junk's " Coleopterum Catalogus " is in its later parts (after 1930) alphabetical within the genus.

Isoptera. Snyder's 1949 " Catalogue of the termites of the world " is alphabetical within the genus.

Mallophaga. The 1952 world list of feather lice by Hopkins & Clay has both the genera (within the family) and the species (within the genus) arranged alphabetically.

Fishes. Gosline's 1945 " Catalogo dos Nematognatos de agua-doce da America do Sul " is in unexplained order. Herre's 1933 list of Philippine fishes is alphabetical within the genus.

Amphibia and Reptiles. Schmidt's North American list (1953) arranges the species alphabetically ; Smith & Taylor's Mexican list (1950) does not.

Mammals. In Allen's 1939 list of African mammals both the genera within the subfamily and the species within the genus are arranged alphabetically. The 1951 list of Palearctic and Indian mammals by Ellerman & Morrison-Scott is in " natural order " and so is that of Ellerman, Morrison-Scott & Hayman on " Southern African mammals " (1953). The latter is explicitly in reaction to Allen's list, which is referred to as " alphabetical and therefore uncritical ".

It can surely be maintained that, though it may have been justified in the past, what is inferred in the last sentence is by no means necessarily true today. In fact I found in my discussions with other systematists a general (though not invariable) disillusion with the putative " natural " sequences, partly because these tended to be delusive and partly because their basis generally appeared to be undocumented, at any rate in that detail which alone would entitle them to respect. In fact, as will be seen from the foregoing sample, an alphabetical sequence of both genera and species is in some favour among workers. As suggested above, it is capable of being readily amplified in such a manner that it achieves the main purpose to which a " natural sequence aspires, without the ambiguity and the unrealistic element that that inevitably entails. The convenience of alphabetical order for ready reference needs no emphasis, but I would advocate that it should as a rule be adopted only when supplemented by the designation of such species-groups as seem to be justified and that no sequence should be put forward unless the justification for it is published.

Among those with whom I have discussed this communication I am especially indebted to Dr David Lack and Dr A. J. Cain.

NOTES AND ABSTRACTS

NOTES ON BRITISH MAMMALS

No. 6

From

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ECTOPARASITES FOUND ON HARVEST-MICE (*MICROMYS MINUTUS* HERMANN)

During the course of threshing a wheat rick at West Bergholt in Essex on 16th December, 1958, sixteen harvest-mice were captured alive. In addition one dead animal was found amongst the outermost sheaves prior to threshing. It appeared to have been dead only a few hours and had an engorged tick (*Ixodes trianguliceps* Birula) attached to the skin behind the left ear and mites (*Laelaps hilaris* Koch) clustered around the anus. One of the live animals also had a tick attached in a similar position. This harvest-mouse was the lightest in weight and its fur did not have the well-groomed appearance of the others.

Ticks transmit infectious diseases of animals, remove blood from their hosts and the bites of a number of species of hard ticks, including some of the genus *Ixodes*, transmit fatal paralysis in animals. In Britain the sheep tick *I. ricinus* (Cameron, 1951) can transmit paralysis. There is considerable discussion however on whether sufficient blood is ever removed from sheep by *I. ricinus* to affect their health seriously (Heath, 1951). Even when the parasites are numerous the transmission of disease may be more injurious than the loss of blood.

Apart from the harvest-mouse, *I. trianguliceps* has also been found on the field vole (*Microtus agrestis*), water-vole (*Arvicola amphibius*), common shrew (*Sorex araneus*) and pigmy shrew (*Sorex minutus*) (Lapage, 1956). It is not parasitic on farm mammals or birds and there is no evidence that *I. trianguliceps* can paralyse its host. If this tick can cause the death of small mammals, it would seem more likely, judging from the physical condition of the live animal captured, to be due to the introduction of an infectious disease than directly to the quantity of blood removed from the host. It is not known whether the harvest-mice were diseased. Even though it is not capable of such enormous extension as *I. ricinus*, *I. trianguliceps* may however remove sufficient blood from small mammals to prove fatal to the host.

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Thanks are expressed to Dr A. M. Hughes who identified the parasites.

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F. P. ROWE.

NOTES ON THE STATUS OF SEALS IN ICELAND, JUNE-JULY, 1959

(1 plate)

These notes on the two indigenous species of seal in Iceland, *Halichoerus grypus* (the Grey seal), and *Phoca vitulina* (the Common seal) were compiled during a visit in June 1959, when a circuit of the island was made by land, sea and air, various modes of travel being necessary owing to the absence of roads in the south-east.

Iceland lies between 63°24′ and 66°32′ N.Lat., and from 13°30′ to 24°32′ W.Long., and notwithstanding the extensive ice caps the climate is not severe as it is influenced by the relatively warm sea current that flows from the south-west along the west and north coasts. The area is about 40,000 square miles, which is some 20 per cent greater than that of Ireland. Generally speaking the shore of the southern coastline is shoal and sandy, whereas the western, northern and eastern coastlines are almost wholly rock-bound.

Grey Seal. "Utselur" in Icelandic.

The stronghold of this species in Iceland is Breidafjordur, a large bay some 40 miles wide in the north-west coastline, which is studded with innumerable rockly islets and skerries. In years gone by many of these small islands were inhabited, and the pups both of this species and *P. vitulina* were cropped annually; but now most of these islets are uninhabited (I believe Flatey is the only one with a human population now) and *H. grypus* is not often killed, mainly because the skin is not valued, except as leather (worth 25 shillings to 40 shillings per skin), and also because it is protected by law. I saw adults of both species in Breidafjordur, during a crossing on 23rd July from Stykkisholmur in the south, to Brjanslaekur in the north, and could judge for myself how suited this area was for them. This is also the main centre of eiderdown collection, a large number of eiderduck breeding on the innumerable islands: about fifty to sixty nests will produce one kilo of eiderdown, and from nests with four eggs one egg is taken for human consumption, but two are taken if there are six or more.

H. grypus is also present along the north and east coasts in small numbers, and in August and September a few pups of this species are born on the sandy shores of the south coast in areas used by *P. vitulina*, but they are not as a rule molested by the sealers, who want the more valuable skins of the latter species.

In Breidafjordur breeding by *H. grypus* takes place in October, and an elderly seal-catcher said that he had once seen a pup in August, and once in February (which lines up with the observations of H. Hewer and K. Backhouse on Ramsey); the moult usually is complete in fourteen days. He had never seen, nor heard, of a seal wearing a metal ring on its hind flipper, and he would certainly have heard if any had been found in that area. Dr Gudmundsson gave me a similar answer regarding rings, and we discussed the Faeroe Island recovery, which is the nearest to Iceland so far recorded. He said that as the adults of *H. grypus* are very seldom killed in Iceland he did not expect to hear of recoveries of marked seals. I gave details of the Zoo's ringing scheme* to two

*In the spring of 1961 a Grey seal was recovered on the south-east coast of Iceland wearing a ring—This is now the furthest north recovery under the Zoo's scheme.

active sealers on the south coast, to Mr Johnsson the principal buyer of seal skins in Reykjavik, and to a sealer in Breidafjordur.

Until fairly recently seal meat was very generally eaten, fresh, dried or salted, by the islanders in Breidafjordur, but it is now seldom consumed. The seal blubber is still melted down and the oil used as a drench for sheep on account of its vitamin content. The hind flippers of both species of seal are kept by the sealers for winter consumption, being pickled in vinegar and eaten as a delicacy.

Common Seal. " Landselskopur " in Icelandic, also " Stenkobbe ".

Along the flat sandy shores of the south coast of Iceland *P. vitulina* breeds in late May and June in considerable numbers. One coastal farmer killed seventy between 10th and 15th June, 1959, due south of Vatnajokull, and another farmer killed sixty-two on the 7th July, 1959, a few miles further eastwards. Most of these were pups, but I saw the skins of some yearlings and adults. Clubs, rifles and nets were used to take the seals. The skins are sold to dealers in Reykjavik, who trade them mostly to Hudson Bay Company in London, where they are dressed and marketed to the Fur trade. The skin of

a Common seal, scraped and air-dried (Fig. 1), will fetch in Reykjavik about £8. 10. 0 for first quality, seconds and thirds are cheaper, usually £7. 10. 0 and £6. 15. 0 respectively. Adults of this species are not so often killed, pups, yearlings and two-year olds being preferred, and skins of older animals and of prenatal pups being used as leather, not as furs.

On the west, north and east coasts the pups of *P. vitulina* are taken in nets at sea, the easiest method of capture, the adults being protected by law I was

told by Dr Gudmundsson of Reykjavik, although there is no protection on the south coast. He also told me that this species is commonly the host of a species of helminth (*Porrocaecum discipiens*) that passes in the course of its metamorphosis from the seal to the haddock, cod and other fish, where it burrows in the flesh, thereby affecting adversely the market values of these fish. Dr Gudmundsson would like to see the population of *P. vitulina* reduced on the south coast, where this worm is prevalent, and where most fish are taken in the trawl, the sea bed being suitable for this method of fishing, unlike the other coastal areas where the trawl cannot be used owing to rocks, and net and line fishing are the rule.

Mr Johnsson, of Reykjavik, who deals in seal skins, told me that he obtains as many good skins as he can get of *P. vitulina* from coastal districts. He calls them " this year's young seals ", but I am sure that some are yearlings, judging from the skin in my possession that I bought from him. He is offered very few skins of *H. grypus* and those that he buys he sells for leather : occasionally he is sent a skin of Harp seal (*P. greenlandicus*), Ringed seal (*P. hispida*), and Blue-backed seal (the pup of the Hooded seal—*Cystophora cristata*), but Iceland is outside the normal breeding area of the three last-named species.

Several farmers living in coastal districts of Iceland engage in sealing as a fairly lucrative addition to their farming activities which, at best, cannot bring them in more than a meagre living. Other farmers in those areas combine fishing, and the collection of sea bird's eggs, with farming. A few years ago a large number of sheep died from disease, or had to be slaughtered, which aggravated the financial position for farmers generally, but new stock was introduced and the situation is now much improved.

The number of seal skins exported (species not specified) for the five years ended 1956, were :

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1953.....2299.
1954.....1812.
1955.....3186.
1956.....2318.

The great majority of seals killed, as represented by these figures, would be *P. vitulina*, and an addition must be made to the totals to include skins for home use, and others that do not find their way on to the market.

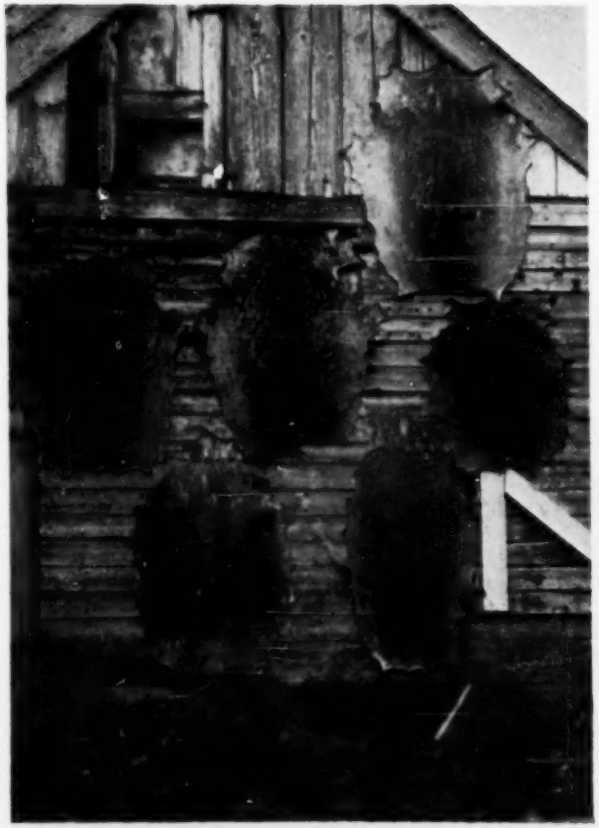
OLIVER HOOK.

" HEADLESS " GREY SEAL PUPS

(1 plate)

From time to time the " decapitated " bodies of grey seal pups have been found on both the Welsh and Northumbrian coasts. In none of the reports, however, were any details available regarding the nature of the " decapitation ".

In May 1956 the authors saw the body of a grey seal pup floating close inshore off the south coast of Ramsey Island, Pembrokeshire. Unfortunately the current did not bring it ashore but detailed observation was made with the aid of binoculars from the cliffs above. As the body was rolled about in the sea it could be viewed from all angles so enabling one very significant point to



1. Skins of *P. vitulina*, at Knapparvellir, South of Vatnajokull. July 1959.

2. The southern coastline of Iceland, near Fagurholsmrei, south of Vatnajokull. This is typical of most of the south coast of Iceland, and near here 62 *P. vitulina* were killed on the 7th July 1959.

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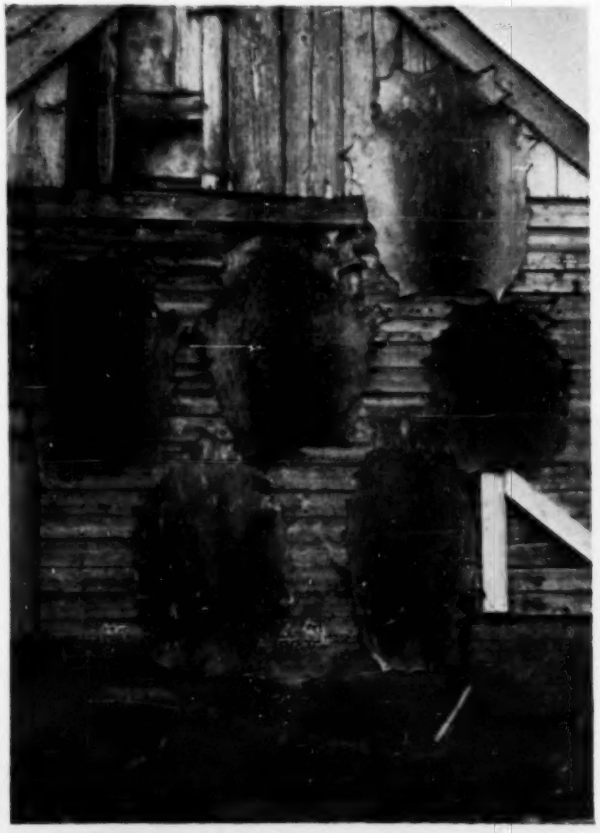

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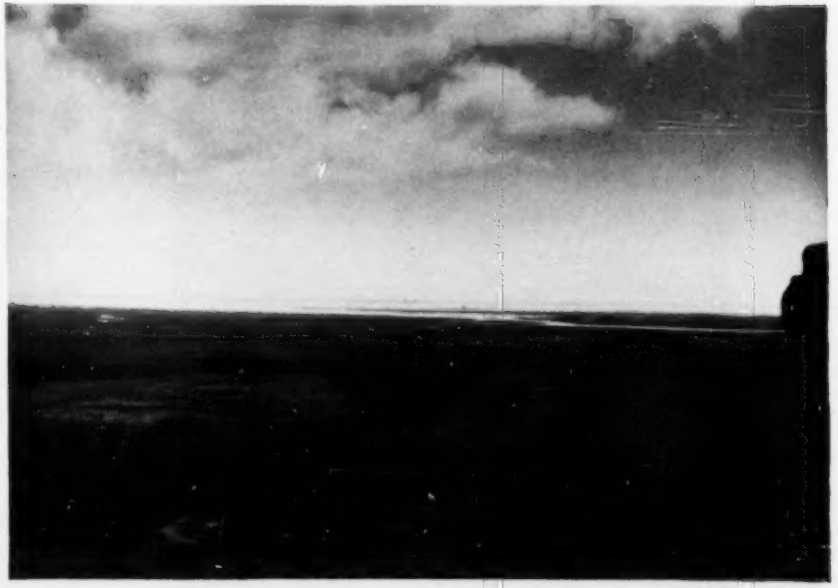

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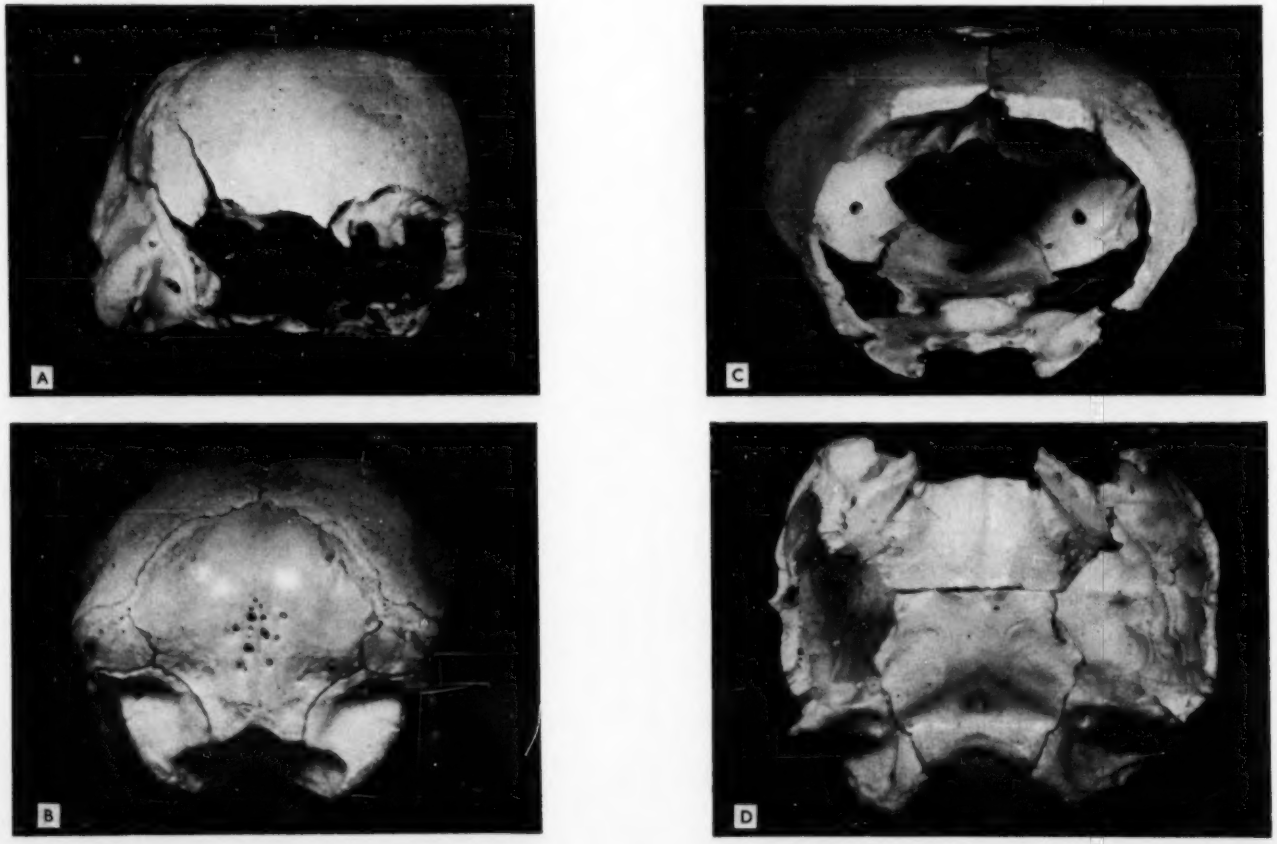

Views of the reconstructed skull of the "decapitated" grey seal pup from Eilean nan Ron: A, lateral; B, posterior; C, anterior and D, ventral aspects. Note that the heavy facial and temporal and otic bones are missing.

be established ; no cut surface could be seen in the cervical area. On the contrary, large dorsal and ventral skin flaps were visible floating freely, anterior to the trunk. Wave action at times showed these extended so that the body appeared to have some sort of head ; at other times the flaps were folded back and little showed in front of the thorax.

This observation suggested to us that the " headless " appearance was due to disintegration of the anterior part of the head with the consequent falling away of the heavy jaw and nasal bones, followed possibly by the rest of the skull. Such disintegration could be caused largely by the carnivorous activity of crustacea attacking the large, soft apertures of the mouth and nostrils.

In September 1957 the authors were on Eilean nan Ron, off Oronsay, Argyllshire. On 22nd September a " headless " grey seal pup was found on one of the beaches after heavy weather. The animal was apparently new-born. In spite of its state of decomposition there was surprisingly little abdominal distension. There was advanced decomposition around the head region and relatively small areas around the anus and umbilicus ; otherwise the white fur was largely intact. The head was, however, not completely lost. The dorsal and ventral skin flaps of the head were practically complete, the eye sockets and the mucous membranous areas of the mouth and nose being virtually the only loss. The tissues of the anterior part of the head were largely lost but the more posterior bones of the skull and the axis and atlas were lying almost free in the decomposed adjacent soft tissues. The ground in the region of the body was searched and other skull bones were found lying free a little way from the body. The posterior part of the skull could thus be reconstructed. Photographs illustrating these points are shown in the Plate. It will be seen that the back of the skull is uninjured so that death was certainly not due to clubbing. More recently one of us (H. R. Hewer) on a visit to North Rona has seen a large number of decomposing bodies of pups in the rock pools. Quite a number of these had nothing more than skin flaps in the head region. A comparable but smaller amount of damage is also seen in the large numbers of dead pups attacked in the eye and mouth region by great black-backed gulls.

We conclude that, in default of any other detailed description of headless seal pups, this appearance is due solely to the normal process of disintegration and decomposition in the sea. Such an observation is in accord with the changes observed in and around the oral region of human bodies after long submersion in the sea.

H. R. Hewer.
K. M. Backhouse.

A SIMPLE LIVE-TRAP FOR SMALL MAMMALS.

While visiting the Laboratoire des petits Vertébrés at Versailles, in 1959, I saw a small mammal trap that had been designed by two members of the staff (M. J. Aubry and the late M. A. Chappellier).

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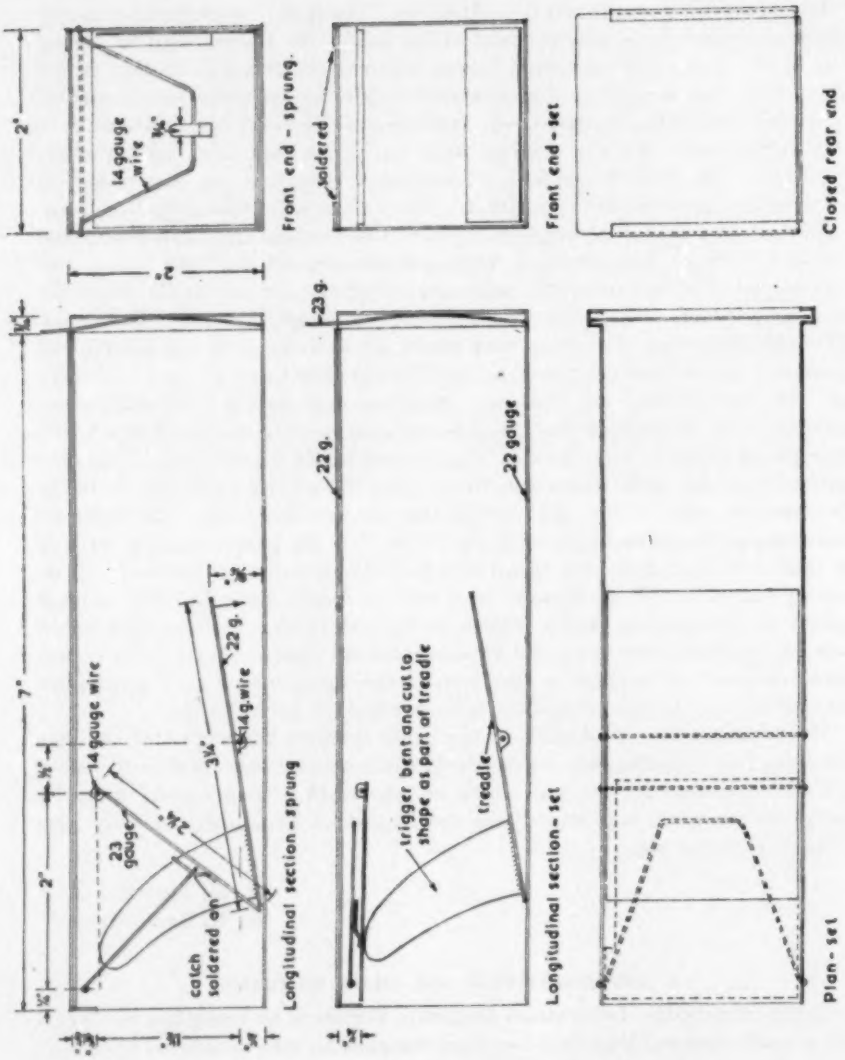

Fig. 1—Trap for small mammals.

house mice (*Mus musculus* L.) field mice (*Apodemus sylvaticus* L.) field voles (*Microtus agrestis* Bellamy) and common shrews (*Sorex araneus* Jenyns).

As the working drawings show (Fig. 1) the trap consists of very few parts—a tunnel, a treadle combined in one piece with the door release, a door, a falling catch to keep the door closed, and a slider at the rear of the trap to facilitate baiting and catch removal. The whole thing is very simple, with few parts that could go wrong or become easily damaged. If made in galvanized metal, the trap weighs 314 grammes against the Longworth's 230 grammes, but it is not readily gnawed by small mammals as the Longworth tends to be.

In practice I found that lengthening the rear part of the trap between the treadle and the slider improves it by allowing more room for bait and a little nest material, and so the working drawings show a tunnel one inch longer than the French prototype. Nevertheless, it is still very compact, and can be inserted into small spaces since it has not the separate nest-box of the Longworth trap.

Monsieur Giban was kind enough to say that there was no intention to patent it but that it could be freely made and used by anyone ; hence this note. I think the trap will prove useful in a variety of environments.

Thanks are due to Mr A. G. Jenson for making the working drawings.

R. A. Davis.

USE OF THE THUMB TO SUPPORT A WHISKERED BAT (*MYOTIS MYSTACINUS* Kuhl) AT ROOST.

Roosting bats when hanging up attach themselves to their roosting place mainly by the claws of the hind feet, a locking mechanism in the muscles and tendons of the digits ensuring that the claws remain at the appropriate angle even when the bat is asleep (Grassé 1955)—indeed bats are not infrequently found dead still hanging from their hind claws. There is no grasping action by the toes : even if the bat is hanging from wires or thin bars of wood of what appear to be suitable diameters for grasping the bat hangs by the claws alone. That the hind claws are used is obvious whether the bat is hanging free from the roof or on a vertical wall but in the latter case it is difficult to see from behind whether the fore limbs are used as well, since they are largely hidden by the bat's body and fur.

A whiskered bat was kept in captivity housed in a wooden box with the back wall made of a sheet of glass against which was fixed a series of horizontal wires 5 mm apart. The same bat was given, in another box and under strong light, the opportunity of choosing as a roosting place one or other of two vertical crevices covered with plain and opaque glass respectively : it showed no preference for the dark crevice (Cranbrook, 1960). It does not seem likely therefore that its roosting habits were affected by being forced to hang up against glass in the light. The bat seldom slept hanging from the hind claws alone but was almost invariably supported by one or both of the thumbs as well, the claw of the thumb being hooked over a wire, the wrist hanging below the wire to which the claw was fixed. Hanging asleep on the wires a geometrically symmetrical position was possible and usual, the msot commonly adopted

being that with both hind feet hooked over one wire the claws of both thumbs over another below, about level with the eyes. In that position the four supporting points were at the angle of an isosceles trapezium with a vertical line drawn through the bat's centre of gravity passing midway between the two hind feet and midway between the two thumbs, so that the weight of the bat was equally distributed between the four. In fact whether the bat hung supported by one, two, three or four of the supporting points provided by the hind feet and thumbs the body was always so adjusted as to bring the pressures on the supporting points used into a similar equilibrium. The claws of the thumbs therefore, save on the occasions when the bat slept hanging from one or both hind feet only, were of importance in supporting the sleeping bat.

When hanging from a vertical side of rough wood the bat always hung with the two hind feet in the same horizontal plane. If the bat arranged itself as it did on the horizontal wires the two thumbs would also be in one horizontal plane, a vertical line through the bat's centre of gravity passing midway between the two. On one such occasion when hanging head downwards asleep on a vertical board the bat must have been supported by the claws of the thumbs alone : it was possible to pass a piece of paper between the hind feet and the board on which the bat was supported. This position, with the centre of gravity higher than the supporting points, could only be maintained if there were some method of keeping the thumbs rigid and at a constant angle to the forearms. The length of the thumb of a whiskered bat, including the claw, is about 7 mm and the angle to the vertical of the fore arm of the roosting bat about 10°. In those circumstances, with the claws of the thumbs hooked into the board and the wrists pressed against it below the point of attachment of the claws, the bat would remain *in situ* with its body slung as it were between the elbows.

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CRANBROOK.

INCREASE OF HARES AT ASHTON WOLD

During the period 1955–1959 the number of hares at Ashton Wold has remained approximately the same. Following the initial increase after the first outbreak of myxomatosis in September 1954 (Rothschild & Marsh 1956) the hare population remained static at about 170–200 animals of all age groups. In the first week of May 1959 four dead foxes were picked up in the woodland area and when the hunting season commenced it became clear that our large population of foxes had been completely wiped out. After the first snowfall the area was carefully checked for tracks but none was found.

The very fine summer of 1959 and the absence of foxes were probably the main factors which contributed to the marked increase in game observed on the estate. The hare population more than doubled in number ; of the 310

animals shot during the winter months, no fewer than 189 were leverets. This constitutes the highest proportion of young to old hares ever recorded at Ashton.

	1954/55	1955/56	1959/60
Hares shot during shooting season	10	101	310
Hares counted after end of shooting season	105	76	120 (Feb.) 90 (May.)
Foxes or fox cubs killed or removed	59	28	4 found dead in May 1959. Covers drawn blank in Nov.

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MIRIAM ROTHSCHILD.

TOILET OF THE HEDGEHOG

It has frequently been stated that the reason why the hedgehog is sometimes heavily infested with fleas and other external parasites is that its prickles prevent it grooming its coat.

All five of my captive hedgehogs scratch themselves. I watched one young male in particular because he was the tamest ; he would scratch himself when his prickles were stuck together after he had self-anointed or if I used talcum powder after washing him or when he had a sore developed among his prickles or fur after fighting with another male. He would raise a hind-leg, balance on the other three and using the longer back toes, would scratch himself vigorously, so that loose spines and mud were scattered over a wide area. His prickles were almost completely relaxed as he did so. He lifted his foot to a point just higher than the irritation and then ran his claws downwards through the prickles. He was able to reach his sides and also the top of his back by hollowing it and throwing the skin into corrugations. Because of his ability to curl up he had so much control over the muscles of his supple skin that he could twitch or pull it in almost any direction, and this much facilitated scratching and self-anointing.

ELIZABETH MAHONEY.

HORN GROWTH IN INFANT ROEDEER

In the year 1931 I picked up in the Greystone Hill Wood, Glen Dye, Kincardine, the bleached skull of a small roe-buck. The head interested me as it had miniature horns *without* coronets. By the size of the head I estimated the animal to be under 12 months of age. There were no jaw-bones or teeth with the skull. Until the finding of this roe skull I had been under the impression that male roe fawns did not throw any antlers until they had reached the

age of between eight to nine months when, in the early months of the year, these youngsters, together with their elder male relatives, would commence to grow their first head adornments ; that is in the calendar year after that in which they were born. Does usually drop their fawns towards the end of May—I say " usually " as there is evidence that some fawns are born several weeks later. From the end of July until mid-August the does come into season again and begin to associate with the bucks. The fawns are now, in nearly every case, able to look after themselves although because of the roedeer's strong family tendencies, fawns may keep with their mothers for a number of years.

Since my first find of the Glen Dye skull I have received a number of specimens of roe heads from various sources and in particular from Lord Richard Percy of King's College, Newcastle upon Tyne and from Mr William Marshall of Nethy Bridge, Inverness-shire. In 70 per cent of these specimens the jaw-bones have been included so that with the help of the British Museum (Natural History) it has been possible to age these roe by their dentition. The old practice of estimating a roe's age by an assessment of the buck's horngrowth is now known to be imprecise. The heads made available by Lord Richard were all shot in March in the county of Northumberland whereas those supplied by Mr Marshall were obtained at the end of November and in mid-December in Inverness-shire.

In four skulls of young bucks supplied by Mr Marshall every one had some degree of horn growth and three out of the four were clean, only one of these three, however, showed any sign of coronet formation, the other two being straight protrusions from the skull pedicle itself. One of these heads was in full-velvet but when artificially cleaned, the horn structure beneath the velvet resembled closely the other specimens. In other words all these four young bucks were carrying horns in November and December. The in-velvet head has been aged at about eighteen months so that the immature horns the buck carried would probably have been the beginning of his second crop of horns. The length of clean horn in the other three bucks varied from a half an inch to two inches.

The two most interesting specimens from the Percy collection were two young bucks, aged by authorities at the Natural History Museum at ten months. These two youngsters were sprouting single spikes still in velvet. Another specimen was from a young buck in velvet shot in April at Cragside in Northumberland. This head has horns over five and a quarter inches in length and allowed to develop and clean would have possibly gone over six inches. There were no forks and, although small, the coronets were distinct. All three of these juvenile bucks aged ten months and eleven months were growing their horns in a normal manner and at the usual time of year for male roe to do so.

In 1956 I was fortunate in being able to spend some days with Professor Harry von Eckermann at his roe-farm at Edeby, near Stockholm. Professor von Eckermann has bred many roedeer. He is quite definite about the growth of horn in infant roebucks. Fawns are born hornless, he says, and it is not until they reach an age of two months or more that slight bumps can be felt on the skull beneath the skin, these bumps rather surprisingly, occur both in the

young bucks *and* the young does. About September (i.e. average age of fawns would be four months) the knobs of the male fawns burst through the skin and clean into hard horn either in the shape of tiny buttons or little spikes. These protuberances are eventually knocked off between the end of December and the end of February.

In the doe fawns small lumps may be felt beneath the skin, where normally the pedicles are to be found in the males, but these remain as knobs and never, except in the rare cases when a female roe grows horns, do they penetrate the head skin. With age these female knobs become more pronounced and in the skulls of aged does are sometimes quite prominent when the head is stripped of its skin. Professor von Eckermann suggests that this phenomenon may be akin to the condition known as adrenal virilism in human beings.

In conclusion, therefore, it would appear that in normal cases the male roe-fawn begins to grow a miniature set of antlers at about four months of age and there can be an appreciable variety in the size, shape and form of this initial head-gear. Soil, food, terrain and milk-availability from the doe, may all influence this early horn growth. Snaffle (1904), has stated that the horns of roedeer are regular only in their irregularity. This would appear to apply just as much to the horns of infant roe as it does to those of adult bucks.

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HENRY TEGNER.

THE RELATIVE EFFICIENCY OF SOME SMALL MAMMAL TRAPS

During August and September 1958 we visited the Val D'Aran in the Spanish Central Pyrenees. One of our objects was to collect small mammals in the area, and we took with us one type of live trap and five different patterns of mousetrap using the breakback principle. Our experiences with these traps in the field, with regard to their weight, size, ease of setting and relative efficiency, may prove useful to other workers.

Description of traps

(a) *Live traps.* The only live trap used was the Longworth Small Mammal trap which is of all metal construction based on the tunnel principle, the animal being caught when it depresses a wire set across the end of the tunnel section. Using these traps with captive animals, it was noticed that occasionally an animal would pass over the release wire both on the way into, and out from the trap, without setting it off, but we have not established that this occurs in the wild. This trap can easily be set in the dark and its release mechanism adjusted to give a very sensitive trip. Size $5\frac{1}{2} \times 3\frac{1}{2} \times 2\frac{1}{2}$ inches. *Price* 17/6d.

(b) *Break-back traps.* All the break-back traps which we took with us measure about $4\frac{1}{2} \times 2 \times \frac{3}{4}$ inches and rely on a spring loaded wire loop which, when released, swings over the base of the trap to pin the animal down across its back, or head, with sufficient force as to kill it instantly. The five types we used differ in their design and materials of construction.

(i) *Sentry trap.* This is one of the many " wooden " mousetraps in which the release is actuated when the bait is moved downwards (it should be noted that the forward gnawing action of a rodent tends to set this type of trap more heavily). Although capable of fine adjustment this is not easily achieved nor is it positive. Difficult to set in the dark. *Price* 5d.

(ii) *Felix trap.* A wood and metal trap in which the forward movement of the bait operates a lever set in the wooden base and releases the fly-over loop. It was found that this lever often became jammed and fine adjustment was difficult to obtain. Not easily set in the dark. *Price* 8d.

(iii) *Little Nipper trap.* This trap is of wood and metal construction and the bait is attached to a wooden treadle, the downward movement of which effects release. The hinging of the treadle is rather sloppy but in spite of this a fine setting can be obtained. It is possible to adjust the height of the treadle by bending the release catch but this trap is not easy to set in the dark. *Price* 10d.

(iv) *Klik trap.* An all-metal trap which operates on a principle similar to that of the Little Nipper except that the treadle is extended as a lever running beneath the base of the trap to the back of the wire loop which is consequently responsive to a much smaller movement of the treadle. It can be adjusted to give a very fine setting and is easily set in the dark. *Price* 1s. 4d.

(v) *Selfset trap.* A very well made metal trap capable of fine adjustment and extremely easy to set in the dark. Release is effected when the bait is moved forward and is equally responsive to a sideways approach. This trap has two springs attached to the fly-over loop and one of these may easily be dis-engaged to reduce the damage to skulls if these are required, although in this case death may not be as quick. *Price* 1s. 10d.

Trapping technique

When all traps were being set on any one occasion they were put down without any conscious preference for any type of trap although at times a break-back would have to be used when the site was too small to admit a Longworth. Since we were interested in maximum yield, the traps were set at what were considered to be the most likely sites and consequently as a result of bad judgment some might be unfavourably placed with respect to the others but over the whole period this would tend to affect all traps equally. Possibly random distribution of the traps along a straight line would produce slightly different results but it is unlikely that the general order of efficiency would be grossly altered. The bait used was either apple or cheese but a greater quantity would be placed in a Longworth trap, together with some bread in the rear compartment which also contained hay as bedding, to keep the captive alive overnight.

Trapping results.

We took a total of twenty-three traps comprising eleven Longworths, four Selfsets, three Sentry, three Little Nippers, one Klik and one Felix and since we caught only sixty-five mammals the data have not been examined statistically.

Table 3 shows a straight comparison when all traps were set on the same occasions and in the same habitats, it will be noticed that the efficiency of the

Table 1—Analysis of all trapping results.

Trap	Trap nights	Number of captures	Number of trap nights per capture
Selfset	57	15	3·8
Klik	16	3	5·3
Longworth	217	35	6·2
Little Nipper	45	6	7·5
Sentry	42	5	8·4
Felix	13	1	13·0

Table 2—Analysis of species caught in each type of trap.

Trap	Trap nights	*Apodemus sylvaticus*	*Eliomys quercinus*	*Microtus arvalis*	*Clethrionomys glareolus*	*Pitymys subterraneus*	*Sorex araneus*
Longworth	217	24	3	5	1	–	2
Selfset	57	9	1	–	1	1	3
Little Nipper	45	4	1	–	–	–	1
Sentry	42	3	1	1	–	–	–
Klik	16	–	–	–	–	–	3
Felix	13	1	–	–	–	–	–

Table 3—The relative efficiency of traps when all were set on the same occasions.

Trap	Trap nights	Total capture	Expected captures per 100 trap nights.
Selfset	*45	13	29
Klik	12	2	17
Little Nipper	36	6	17
Longworth	132	17	13
Sentry	36	4	11
Felix	12	1	8

* All available traps were set on each of twelve occasions but one Selfset was lost making the total number of settings for this make 45 instead of 48.

Longworth trap with respect to the Little Nipper is in the reverse order to that shown in Table 1. This can be explained by the sole use of the Longworth traps on some occasions when live specimens were required.

When purchasing traps for this work it should be borne in mind that the expected life of the different kinds will vary considerably ; a factor to take into account in any long term project. Obviously the wooden traps will have the shortest life as they soon warp although the Felix trap was the only one to suffer in this way as a result of occasional soakings and heavy dew during the course of one month's use. This could usually be cured by allowing the trap to dry out thoroughly between settings.

Of the metal traps the Longworth would be expected to have the longest life since all the working parts are enclosed and the body is of alloy construction but owing to its larger size it has to be more carefully camouflaged if used in areas to which the public have access as it is likely to be interferred with, or even removed. In its favour the Longworth trap is the only one which can safely be used in the vicinity of domestic animals unless the greatest care is exercised in the selection of sites, or the break-backs are covered in some way. In any case there is the risk of damage to traps which are set in fields used by cattle.

Since the data are so few it has not been possible to determine whether any particular type of trap is the most efficient for taking a given species of mammal. It would be expected that traps not capable of being finely adjusted would fail to be released by the lighter mammals e.g. shrews although they may be responsive to the heavier species e.g. field mice. This is supported (Table 2) by the fact that the only wooden trap to catch a shrew operated on a treadle principle where the movement of the release catch is magnified.

In a total of thirty animals caught in break-back traps, four had the skull badly damaged but in no case was the skin broken by the action of the trap. In two cases the carcase had been partly eaten during the night, probably by beetles (on one occasion two carabids were present on the carcass when the traps were collected). Mammals caught in Longworth traps were always undamaged but since six break-backs could be carried in the space required by one Longworth and further, since the cost of break-backs is so much less, this is not a great advantage.

In conclusion it would appear that from considerations of cost, size and efficiency, the metal break-backs are the most useful traps to take on a mobile collecting trip but a small amount of wastage due to damaged specimens must be expected. The larger, heavier and more costly Longworth trap is of course essential if live specimens are required and is the better type of trap to use if ectoparasites are being collected since many of these leave the host as soon as the body chills. A combination of a few Longworth traps and many break-backs is probably the best arrangement, the numbers of each type being varied to suit the nature of the study and the type of ground to be covered.

G. C. Phillips.
K. East.

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